INTERPRETATION OF EUHAPSINE (CASTORIDAE: PALAEOCASTORINAE) BURROWING BEHAVIORS BASED ON THE FUNCTIONAL ANATOMY OF THE TEETH AND SKULL WITH A DESCRIPTION OF A NEW SPECIES AND GENUS

By

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Submitted to the graduate degree program in Geology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

The systematics and burrowing behaviors of the Oligocene–Miocene palaeocastorine beaver tribe Euhapsini are reviewed. A new species, *Euhapsis martini*, is described based on material from South Dakota previously attributed to an exclusively European radiation. A new genus, *Paraeuhapsis*, is described for the previously recognized *E. breugerorum* and *E. ellicottae*, based on the unique cranial morphology relative to the other euhapsine beavers. *Paraeuhapsis* is shown to differ from *Euhapsis* on the basis of the following characters: upper incisors with longitudinal grooves, deeper rostrum, thickened and noticeably rugose nasal bones with a boss, and protrogomorphic skull arrangement. The functional anatomy and burrowing behaviors of the euhapsine beavers are investigated based on comparisons with extant rodents and other fossil rodents belonging to the Palaeocastorinae and Mylagaulidae. The function of the grooved upper incisors is investigated, and the function of the teeth is determined to correlate with a preference for a grazing diet, rather than a function to increase tooth strength or ease its removal from soil. The morphology of the upper and lower incisors is investigated in modern rodents, and though the lower incisors do not appear to have any correlation with burrowing behavior, the width:length ratio, degree of procumbency, and wear-facet morphology of the upper incisors are all shown to correlate with burrowing behavior. These correlations are applied to fossil taxa to interpret chisel-tooth-digging behavior in most palaeocastorine beavers (e.g., *Palaeocastor fossor*), and head-lift-digging behavior in the euhapsines *Euhapsis* and *Paraeuhapsis* and the mylagaulids. The structure of the unique nasal bones of *Paraeuhapsis* is investigated using epi-illumination microscopy and micro-CT scanning. *Euhapsis* is demonstrated to possess a broad rhinarium whereas *Paraeuhapsis* is demonstrated to possess a

keratin fiber horn, based on comparisons with modern subterranean rodents and living rhinoceroses.

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INTRODUCTION

OVERVIEW

This dissertation arose from a project begun by Professor Larry Martin to revise the systematics of the tribe Euhapsini, a clade of palaeocastorine beavers erected early in his career (Martin, 1987). The palaeocastorine beavers are some of the most well-known fossil rodents, due to their associated trace fossils—the giant, cork-screw burrow *Daemonelix* constructed by the taxa *Palaeocastor* and *Pseudopalaeocastor* (e.g., Schultz, 1942; Martin and Bennett, 1977). Studies on euhapsine beavers remain limited due to limited occurrence and diversity of fossils.

Peterson (1905) named the genus *Euhapsis*, which received no attention until the systematic revisions of Stirton (1935) and Martin (1987). Xu (1996) named a new species; otherwise the group has only been considered in systematic reviews for the family Castoridae (i.e., Korth, 1994, 2001; Xu, 1995, 1996; Rybczynski, 2007; Flynn and Jacobs, 2008). Discussions of evolution relating to burrowing behavior were made by comparison to the better known *Palaeocastor* (Rybczynski, 2007; Samuels and Van Valkenburgh, 2009). The two additional species recognized by Martin (1987)—*E. breugerorum* and *E. ellicottae*—were demonstrated to be different from the type of the genus, but mostly due to the lack of additional material, all the known species were referred to a single genus. The recognition of a new species by Xu (1996) and an additional specimen (AMNH 10818) that is herein demonstrated to be a euhapsine rather than a castorine beaver demonstrates that there is significant morphological diversity within the genus *Euhapsis* as it was previously recognized. This dissertation begins with the description of a new species of *Euhapsis* based on AMNH 10818 and erects a new genus based on some of the *Euhapsis* material previously described by Martin (1987). The recognition of the new genus is necessary not only to classify the diversity of form as is now

recognized, it also has serious implications for the understanding of the evolution of rodent cranial muscles.

Martin (1987) recognized that the euhapsine beavers were among the most fossorial rodents ever known. At the time the tribe was erected, however, understanding of the convergence of form in modern burrowing mammals was only beginning to be understood (e.g., Hildebrand, 1985), so while many of the interpretations made by Martin (1987) were correct, they need to be contextualized based on the continuing research undertaken by modern ecologists. For example, Martin (1987) described the euhapsines as tooth diggers, based on their external, procumbent incisors. While this is likely correct, rodents use their incisors in two dramatically different behaviors that vary strongly with soil type, so further interpretation of the behavior of the euhapsines based on their cranial anatomy is both necessary and now possible. The euhapsines are compared in this study to numerous modern and extinct burrowing rodents to attempt to interpret their behavior (Fig. 1).

The diversity of form represented by the additional taxa described herein has further implications for the interpretation of burrowing behavior for this group. One of Martin's legacies has been to establish the role of iterative climate change as a governing force in repeated evolution of ecomorphs (e.g., Martin and Meehan, 2005). Part of this dissertation will refine Martin's (e.g., Martin and Naples, 2002; Martin and Meehan, 2005) interpretation of repeated evolution of burrowing rodent ecomorphs.

The synapomorphy that unites all rodents is the single pair of ever-growing upper and lower incisors that are isolated from the remaining cheekteeth by an enlarged diastema (Feldhammer et al., 2007). The incisors are never in occlusion at the same time as the cheek teeth


A1
A2
B1
B2
C1
C2
D1
D2
E1
E2

Figure 1—Representative taxa examined in this study to compare with euhapsine behaviors. Skulls depicted on the left (X_1), and live modern specimens or reconstructed skeletons of extinct specimens on the right (X_2). A) *Geomys bursarius*, a modern geomyid that use scratch digging behavior, B) *Heterocephalus glaber*, a modern bathyergid that uses chisel-tooth digging behavior, C) *Nannospalax* (*Spalax*) *leucodon*, a modern spalacine that utilizes head-lift digging behavior, D) *Palaeocastor fossor*, an extinct castorid interpreted to use chisel-tooth digging behavior, E) *Ceratogaulus minor*, an extinct mylagaulid interpreted to use head-lift digging behavior. A_2, B_2, C_2, and E_2 courtesy of wikimedia commons, D_2 modified from Peterson (1905).

as a result of this morphology. Rodent incisors are also unique since the enamel covers only the labial surface of the tooth, leaving the dentine exposed on the lateral and lingual margins. Because enamel is harder than dentine, the distal ends of rodent incisors naturally wear into chisel shapes as they are used in life. The teeth are thereby selfsharpening with the enamel of the lower teeth wearing the dentine of the upper teeth and vice versa. These permanent and rapidly growing teeth are utilized to process food items and in some rodents to dig burrows. The growth rate of the incisors is proportional to the wear rate; therefore, longer incisors correlate with high usage (Rinaldi and Cole, 2000). Different incisor morphologies relate to diet and burrowing behavior. The architecture—degree of procumbency, proodonty, length:width ratio, shape of the wear facet—of burrowing rodent incisors and its relationship with burrowing are described in this study as well.

Perhaps even more important for rodent systematics and functional anatomy, the occurrence of a unique masseter arrangement in the newly described genus of euhapsines impacts our understanding of rodent evolution. The modification of the rodent masticatory

apparatus to enhance the anteroposterior movement of the lower jaw gives rodents their characteristic ability to gnaw (rapidly bite using the incisors). This characteristic gnawing ability gives rodents their name (i.e., 'rodere' is Latin for gnaw). There are four patterns of masticatory muscle arrangements (protrogomorphy, sciuromorphy, myomorphy, and hystricomorphy) observed in rodents and these have served as the basis for systematic classification (e.g., Simpson, 1945; Wood, 1955; Korth, 1994; Vaughan et al., 1999; Feldhammer et al., 2007; Janis et al., 2008). Recent discoveries, however, cast doubt on the utility of these schemes and show that the complexities and convergent patterns of rodent evolution are far more complicated than considered previously (e.g., Cox et al., 2012). This dissertation will elucidate some of these complexities and describe the utility of the protrogomorphic state as a useful derived character state employed by burrowing taxa rather than as a primitive evolutionary holdover (e.g., Arjo, 2007).

SUMMARY OF FAMILY CASTORIDAE

Beavers (family Castoridae) are among the most recognizable modern rodents. Modern beavers are characterized by a broad, flat tail used as a paddle, webbed hind feet, relatively large size (i.e., the second largest extant rodent), and their capacity for secreting castor oil to waterproof their fur (Nowak, 1999). Perhaps the most iconic aspect of the beaver is their tremendous ability to cut down trees with their teeth for the purpose of dam and lodge construction. Beavers are rightly described as one of nature's most prominent ecosystem engineers (e.g., Baker and Hill, 2003), and apart from humans, beavers are perhaps only bested by ants and termites in their ability to transform the environment to suit their own needs. There are only two extant species of beaver—*Castor canadensis* from North America and *Castor fiber*

from Eurasia—both of which display similar affinities for tree-cutting and a semiaquatic lifestyle (Nowak, 1999). Castoridae, however, has a long fossil history extending to the Eocene, and many members of this family were adapted to burrowing rather than to life in the water (Flynn and Jacobs, 2008).

Castoridae can be split into several subfamilies. The Agnotocastorinae are the earliest beavers, variously considered to be generalists and semiaquatic specialists (Korth, 2001). The subfamily Castorinae includes the modern *Castor* and its closest relatives, many of which likely exploited trees for food and shelter (Korth, 2001; Rybczysnki, 2007). The subfamily Castoroidinae was the lineage that ultimately gave rise to the giant beaver, *Castoroides,* but also included a clade that became specialized for tooth digging behavior (Korth, 2007a, 2007b). Both Castorinae and Castoroidinae are thought to be semiaquatic specialists (Rybczysnki, 2007). The Migmacastorinae are an intermediate group composed of a single genus adapted for burrowing that is not closely aligned with any other subfamily (Korth and Rybczynski, 2003). The subfamily Palaeocastorinae diverged in the late Oligocene and diversified in the early Miocene (Martin, 1987) at a time when the climate dramatically cooled and dried, producing widespread grasslands (Retallack, 2001, 2007). All members of the Palaeocastorinae were likely burrowers, with various species specialized for every known type of modern burrowing behavior (Samuels and Van Valkenburgh, 2009). Paired side-by-side with the modern forms, one would probably be hesitant to label a paleocastorine as a beaver, given their tremendous superficial dissimilarity from the modern *Castor*.

Palaeocastorines can be recognized on the basis of several characters (Martin, 1987). The incisors have a flattened anterior surface—in contrast with a convex anterior surface characteristic of castorines and other rodents. The incisors were procumbent and emerged

outside of the closed lips (proodont) as in modern pocket gophers (Geomyidae) and mole rats, which are actually neither moles nor rats; “mole rat” is rather a broad ecomorphic term for several types of blind burrowing rodents. The incisors of most species lack the prominent orange color that characterizes the iron-rich incisors of modern *Castor*; this is a trend observed in a variety of extant burrowing rodents in which increased burrowing capacity correlates with fainter enamel color (Stein 2000). An additional character noted by Martin (1987) is the tendency of P4 to develop three lingual lakes and a labial reentrant. Palaeocastorines can be further diagnosed by the reduction of the tail, again similar to that seen in such modern burrowing rodents as prairie dogs (*Cynomys*), pocket gophers, and mole rats.

The earliest beavers (subfamily Agnotocastorinae) were likely semiaquatic. This has been interpreted based on the occurrence of their fossils in deposits interpreted as ponds and backwater environments (Martin, 1987). Korth and Rybczynksi, (2003) reviewed this interpretation, and determined while it was difficult to unilaterally determine environmental habit from the depositional environment, the cranial morphology of *Agnotocastor* was too generalized for a fossorial habit. The split between the Castorinae and Palaeocastorinae occurred in the Oligocene, when drying climate opened burrowing niches (Martin, 1987). The ancestor of the Palaeocastorine beavers achieved success on the floodplain rather than in the stream channel, and later evolved to life underground. The castorines, on the other hand, continued to have success as semiaquatic browsers, and diversified into many different forms, including the giant marsh specialist, *Castoroides,* and the modern, tree cutting *Castor*.

Euhapsini (Martin, 1987) is one of two recognized tribes of Palaeocastorinae. The euhapsines are recognized by the presence of a pit on the rostrum anterior to the zygomatic, restriction of the origin of the superficial masseter muscle to underside of the zygomatic, and

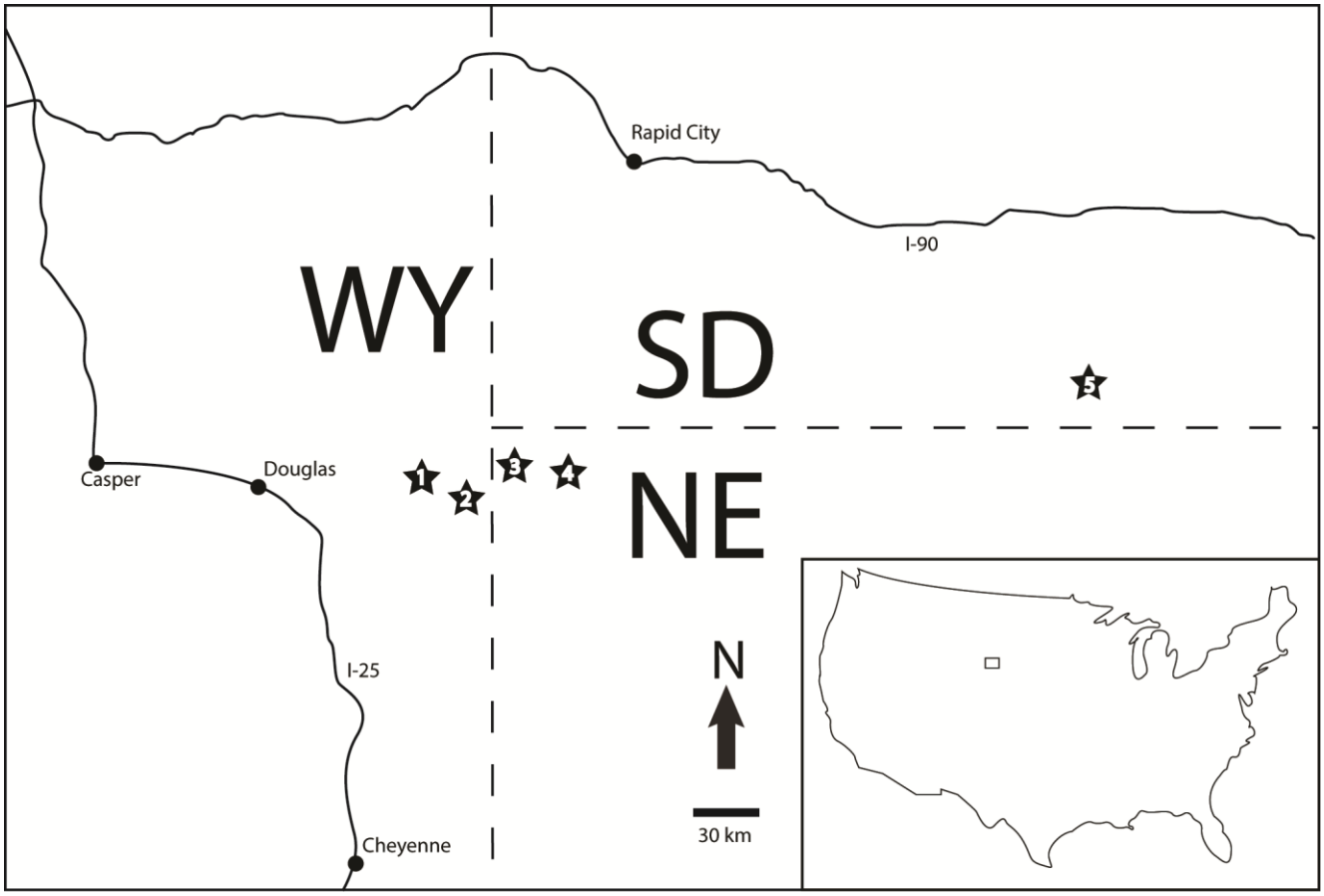

Figure 2—Map of occurrences of euhapsine fossils in the Central Great Plains of North America: 1) Latest Arikareean, near Lusk, Wyoming; 2) Harrison Formation, KUVP Coll.Loc.Wy-115, north of Van Tassell, Wyoming; 3) Harrison Formation, KUVP Coll.Loc.Neb.-31; 4) Monroe Creek Formation, Sioux Co., Nebraska; 5) Monroe Creek Formation near Rosebud Reservation, South Dakota.

short, wide skulls. The genus *Euhapsis* (Peterson, 1905) is the type for the tribe, and the type species *E. platyceps* can easily be recognized by the wideness—skull length is nearly equal to the zygomatic breadth—and flatness of the skull. The euhapsines were a late Oligocene and early Miocene radiation, and they are known only from the Great Plains region of North America (Fig.

2). Four species of *Euhapsis* are currently recognized: *E. platyceps*, *E. breugerorum*, *E. ellicottae*, and *E. luskensis*. In addition to the wideness of their skulls, a defining characteristic of these derived euhapsines is a rostral expansion of the glenoid fossa—the articulation of the upper skull with the lower jaws—into the occipital region of the skull. This feature is unique to euhapsine beavers (see Chapter 2 for a discussion of the utility of this feature) and the modern spalacines *Spalax* and *Nannospalax* (Krapp, 1965). At present, there is a diversity of forms within the genus *Euhapsis*, where some species have highly flattened skulls (*E. platyceps* and *E. luskensis*) and other species have somewhat taller skulls with thickened nasal bones ("*E". breugerorum* and "*E." ellicottae*). Chapter 2 of this dissertation contains a description of a new species of *Euhapsis* which warranted the erection of a new genus to separate the taller skulled euhapsines from those with highly flattened skulls. The remaining genus, *Fossorcastor*, lacks the specialized glenoid fossa of the other two genera. Chapter 2 also provides a phylogenetic analysis of the euhapsine taxa.

INTERPRETATION OF BURROWING BEHAVIOR IN RODENTS

Digging behavior is used by many rodents for a variety of reasons, for example creating shelters or dwellings and locating, storing, and retrieving food (Nowak, 1999), so some care must be taken when applying terminology to burrowing rodents. The terminology of Hildebrand (1985) has been popularized and is utilized herein. 'Fossorial' means specialization for digging while 'burrowing' means constructing an open tunnel system. 'Subterannean' (Hildebrand, 1985; Lacey et al., 2000) or 'hypogeal' (e.g., Pirlot, 1990) means an animal spends the majority of its life below the ground. As such, there are fossorial mammals that are not burrowers (e.g., anteaters, *Sciuris niger*), there are subterranean mammals that are sand swimmers and therefore

not burrowers (e.g., golden moles), there are subterranean mammals (e.g., weasels) that are neither fossorial nor burrowing that merely exploit tunnels created by other animals to find and trap prey, and there are burrowing mammals that are not considered subterranean, such as badgers (*Taxidea*) and ground squirrels (*Spermophilus*). For simplicity, subterranean rodents will be contrasted with 'epigeal' rodents, which will be defined as rodents that spend a majority of their lives above ground completing such essential tasks as gathering food and seeking new sites for burrowing. Rodents considered to have subterranean lifestyles are the primary focus of this dissertation. Some attention is also payed to *Aplodontia rufa*, which is a burrower but is not truly subterranean. It is the only living protrogomorph and member of the Apldontidae, which inhabits the Pacific Northwest of North America and specializes on montane environments (Verts and Carraway, 1998).

Modern mammals use one of six different burrowing styles, and three of these behaviors are utilized by various members of the Rodentia (Fig. 3; Hildebrand, 1985). Scratch digging is the primitive style of digging that requires only somewhat enlarged forelimb claws. As such, nearly every species of rodent is capable of at least some type of digging behavior, even though only a small portion of modern rodents are subterranean (Hildebrand, 1985). Head-lift digging is another burrowing style; in this mode, the soil is broken free by twisting action of the head. The loosened soil is then either thrust away from the body by the head or kicked away by the feet. Commonly observed adaptations in rodents using this style of burrowing are forward (i.e., anteriorly) angled occipital bones, utilized to attach the strong muscles needed to thrust the soil, and nose pads, which serve as shock absorbers to protect the skull from damage during burrowing. Chisel-tooth digging, which as the name implies, involves the use of the incisors to gnaw at the soil. The upper incisors brace the skull to the roof of the burrow while the lower

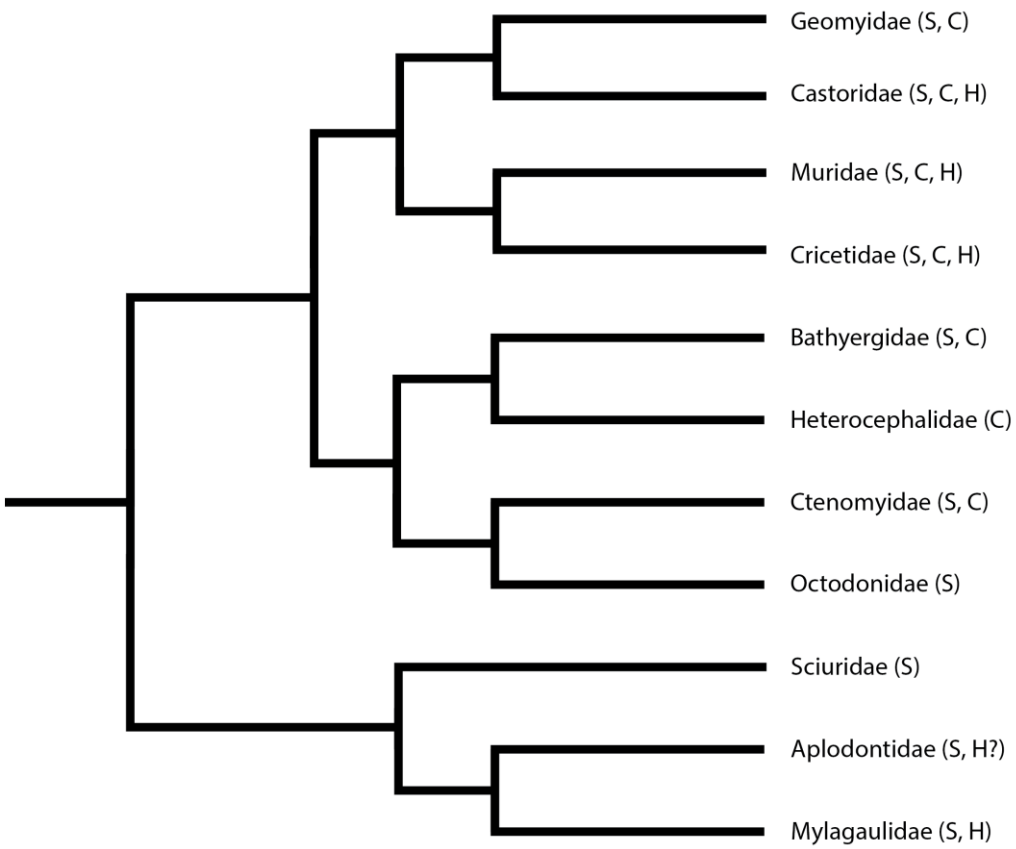

Figure 3—Phylogeny of subterranean and notable burrowing rodent families, including all modern families and extinct families of North American subterranean rodents. Burrow behavior utilized by differing species of the family indicated in parenthesis: S = scratch digging, C = chisel-tooth digging, H = head-lift digging.

incisors perform the chiseling action. The removal of the soil varies among different species, but the soil is generally brushed out of the burrow by the feet in chisel-tooth digging rodents (Jarvis and Sale, 1971; Stein, 2000).

Subterranean lifestyles evolved in several groups of living rodents. No subterranean rodents currently live in Australia. Two families occupy the subterranean niche in South America, Octodontidae (only the species *Spalacopus cyanus*) and Ctenomyidae, which is the

most speciose family of burrowing rodents (Lacey et al., 2000). Numerous groups in Eurasia occupy the subterranean niche (Lacey et al., 2000): the mole voles (Cricetidae, Arvicolinae), zokors (Spalacidae, Myospalacinae), bamboo and root rats (Spalacidae, Rhizomyinae), and mole rats *sensu stricto* (Spalacidae, Spalacinae). Some rhizomyines and spalacines have African distributions as well. The modern representatives of the families Bathyergidae and Heterocephalidae, known from Africa, and Geomyidae, known from North and South America, are all subterranean. A summary of the evolution of subterranean rodents in North America is provided in Chapter 4.

The skull is the most specialized structure of the mammalian skeleton, and its adaptations strongly reflect the environment in which the organism lives (e.g., Wake, 1993; Nevo, 1999), its diet (e.g., Hiiemae and Crompton, 1985; Smith, 1993; Samuels, 2009; Esselstyn et al., 2012), and in some cases even its gender (e.g., Prothero, 2005). Subterranean mammals have several unique modifications of the skull that reflect their enhanced capacity for burrowing. Many different lineages have evolved procumbent incisors that emerge outside of the lips, creating the cheek pockets of pocket gophers. This change is also reflected in the skull by the presence in some taxa of a rostral fossae utilized as a site of muscle attachment for the lip retractors. Subterranean taxa generally have reduced external pinnae, reflected on the skull by a reduction of the auditory meatus below the surface of the temporal bones. The nasal bones of some burrowing mammals are widened, elongated, and bear a rugose texture, and they reflect the means by which the organism digs through the soil.

There have been numerous attempts to quantify the alterations of skull morphology as a way to interpret digging behavior and to interpret this behavior in extinct mammals. Van der Merwe and Botha (1998) studied African mole rats (Bathyergidae) and determined that the

enamel thickness of the incisors and the procumbency of the incisors had a strong relationship with digging behavior. Korth and Rybczynksi (2003), presented two different metrics for evaluating incisor procumbency—incisor angle relative to diastema length and incisor angle relative to tooth row length—both of which were used as positive evidence for interpreting chisel-tooth digging behavior in the bizarre early castorid *Migmacastor* and a unique clade of castoroides (Korth 2007a, 2007b). Samuels and Van Valkenburgh (2009) utilized a more comprehensive approach to evaluate skull morphology of burrowing beavers. They found a similar conclusion that procumbent incisors correlate with chisel-tooth digging behavior. They were unable, however, to completely resolve the burrowing behavior of the tribe Euhapsini, which is the focus of the present study.

Euhapsine beavers may have been the most fossorially adapted of any known group of rodents. Though most euhapsine taxa are known only from cranial material, the head is still considerably modified for burrowing habits; the following section and Table 3 of Chapter 2 list the cranial features of rodents that correlate with burrowing ability. A likely cause for the inability of Samuels and Van Valkenburgh's (2009) model to predict burrowing behavior for some euhapsines is that their skulls possess so many adaptations that are not seen together in any modern rodent taxa. Many studies have independently concluded that the angle of incisor eruption is an indication of burrowing style (e.g., Lessa, 1990; van der Merwe and Botha, 1998; Samuels and Van Valkenburgh, 2009); rather than test that conclusion, it will be used as an assumption to test the validity of other measures of cranial adaptation as proxies for burrowing style.

BURROWING ADAPTATIONS IN RODENTS

The anatomy of burrowing rodents and its relationship to burrowing behavior has received considerable attention and has been consolidated in several excellent reviews (e.g., Hildebrand, 1985; Wake, 1993; Nevo, 1999; Stein, 2000). The limitations of a subterranean lifestyle are reflected in the skeleton. All subterranean rodents have fusiform bodies—the body is the same diameter as the head and the limbs are short and stout (Stein, 2000). Tails tend to be highly reduced, and many burrowing rodents are tailless. The pelage is short—absent in the case of the naked mole rat—but the vibrissae are elongated, more abundant, and occur on the body. Pelage color is variable, however, and likely corresponds with such numerous environmental factors as humidity and soil color with the purpose of enhancing crypticity (Nevo, 1979; Stein, 2000). The head and forelimbs are the primary components of the skeleton that are modified in burrowing species. The limbs of all burrowing rodents are short, but the limbs become more stout, the scapulae broaden, and the claws are enlarged in those rodents using scratch-digging and head-lift digging behavior (Stein, 2000). There are some postcranial elements associated with the holotype of *Paraeuhapsis breugerorum* (KUVP 28376) that do correspond well with the interpretation of head-lift digging behavior detailed in this dissertation (see also the original description of this specimen in Martin, 1987). Most euhapsine beavers are known from cranial and mandibular elements only, so the majority of the anatomical discussion of this dissertation will pertain to adaptations of the skull.

The overall proportions of the skull are highly modified in burrowing rodents. Epigeal rodents generally have tall, narrow skulls; the skull of a rat or squirrel appears pointed as a result of these proportions. Burrowing rodents, by contrast, are somewhat flatter and much wider than those of epigeal rodents. The skull becomes flattened as a means of diminishing body size and, therefore, decreases the cost of burrowing. The wideness of the skull is created by the increased

breadth of the zygomatic arches, which serve as the attachment sites for many of the jaw-closing muscles (e.g., temporalis, masseter, zygomaticomandibularis). The squamosals (part of the attachment site for the temporalis) in particular become enlarged, and this increase in size typically forces a reduction (or elimination) of the interparietal bone. These changes in part compensate for the diminished space for muscle attachment formed as a result of the flattening of the skull. The jaw-closing muscles of all burrowing rodents are dramatically enlarged to better cut roots, to process geophytes, and to move large obstacles out of the path of the burrow. Chisel-tooth digging rodents are even more highly modified as the teeth are the primary digging apparatus. In some burrowing taxa, the already highly modified masseter arrangements are further modified to enhance burrowing capability. The mountain beaver (*Aplodontia rufa*) is the only living protrogomorph; this potentially relates to its digging capabilities (e.g., Druzinsky, 2010). The skull is also modified to increase the size of the neck muscles in chisel-tooth digging taxa, and even more so in head-lift diggers. The nuchal crest is enlarged to create more space for the attachment of the neck muscles. The occipital region is considerably widened, extending in some cases onto the zygoma, and is titled forward. This dramatically increases the space of attachment for rhomboideus cervicis, the neck muscle responsible for the elevation of the head and neck. This muscle is dramatically enlarged in some head-left diggers (see figure 6-6 of Hildebrand, 1985); one such head-lift digger, *Nannospalax* (*Spalax*) *leucodon* has been described as having a "bull" neck (Watson, 1961).

The sensory apparati of subterranean rodents are also highly modified. Subterranean rodents spend most or all of their time below ground in low or zero light conditions, and the sense of sight is reduced (Stein, 2000). The eyes are therefore reduced in size, reflected skeletally by a reduction in the size of the orbit. Many burrowers also have more dorsally situated orbits.

Some subterranean rodents (e.g., *Spalax*, *Nannospalax*) have a layer of skin that grows over the eyes, permitting them to only determine the difference between light and dark (Nevo, 1999). Bathyergid rodents have coopted the use of the eyes as a tool to sense openings in their burrow systems. The lacrimal fossa and gland are enlarged to increase the ability to moisten the eyes, increasing the ability of the eyes to detect air pressure and wind changes in the burrow system (Eloff, 1958). The occurrence of these same characters in euhapsine beavers was noted by Martin (1987), and the functional significance in euhapsines is discussed in Chapter 2 of this dissertation. The auditory bullae—resonating chambers made of bone to amplify sound waves—are inflated in burrowing taxa to improve the ability to detect low frequency sounds that travel through the ground. Extant *Spalax* have been observed to communicate using low-frequency sound waves (Nevo et al., 1991).

The teeth of all subterranean rodents are highly modified. The incisors are external to the oral cavity (proodont), so the lips close behind the incisors and they are visible even when the mouth is closed. Pocket gophers and pocket mice (Heteromyidae) are the only modern rodents with fur-lined cheek pouches anchored to the rostrum by laterally-facing deep pits; however, euhapsines also possess pits on their rostra that may be consistent with these types of pouches. This, in concert with the enlarged jaw muscles, enhances their ability to move obstacles (e.g., small rocks) and cut roots and plants, even in those taxa that do not rely on their teeth as the primary digging tools. The incisors are frequently procumbent, primarily in chisel-tooth digging taxa. The increase in procumbency occurs as a result of the arc of the tooth growth increasing and the root end of the tooth shifting caudally. The roots of many chisel-diggers extend beyond the molars, and in the lower jaws, an additional process (capsular process; Fig. 4) is formed when the root approaches the surface of the bone. The incisors of most burrowing rodents are

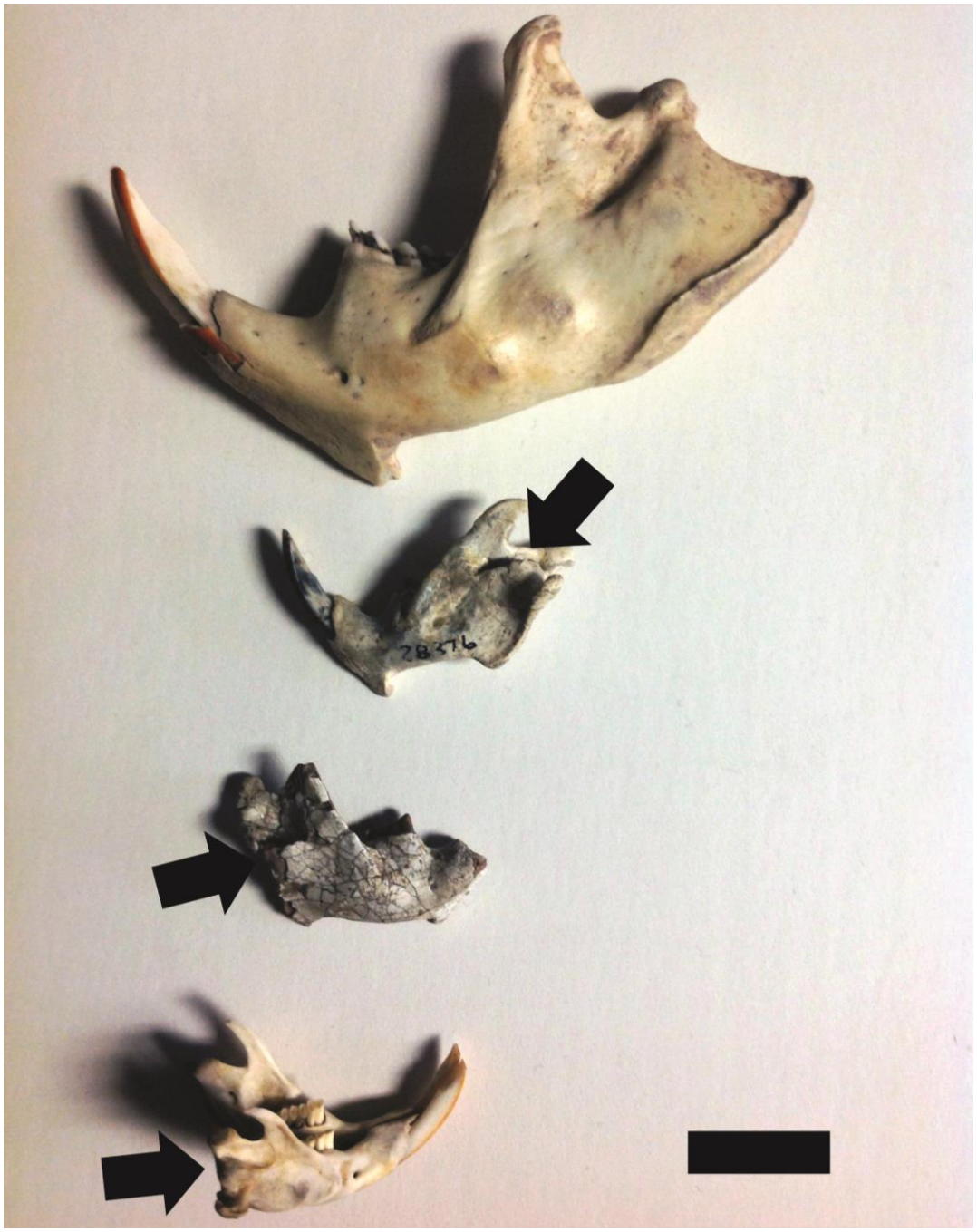

Figure 4—Comparison of rodent mandibles showing the capsular process of burrowing species. Top to bottom: *Castor canadensis*, *Paraeuhapsis breugerorum* gen. nov., *Euhapsis martini* sp. nov., and *Geomys bursarius*. The capsular process (arrows) is enlarged in *Geomys* and absent in *Castor*. The euhapsines either possess a capsular process or the tooth root can be seen at the surface of the damaged bone of the mandible. Scale bar 5 cm.

characterized by thicker enamel (van der Merwe and Botha, 1998) and higher growth rates by comparison to epigeal rodents (Howard and Smith, 1952; Miller, 1958; Manaro, 1959). Digging in the soil increases the wear rate of the incisors, so these modifications offset the increased attrition. The elongation of the incisor socket further helps to alleviate the increased wear rate of the teeth. Many burrowing taxa bear grooved upper incisors, whereas the typical rodent incisor has a smooth labial surface. The significance of this character for rodent functional anatomy is discussed in Chapter 3, and its utility in interpreting behavior in fossil rodents is discussed in Chapter 4. The cheek teeth are hypsodont (high-crowned, and sometimes ever-growing) in most burrowing rodents; this reflects the change in food supply from seeds (which are a dominant food source of epigeal rodents) to grass, roots, and other tough subterranean plant growths (e.g., Stein. 2000).

Burrowing rodents have much larger nasal growths than epigeal rodents. Many subterranean rodents have valvular nostrils to prevent soil from entering their nasal passages as they burrow (e.g., Stein. 2000). The nasal bones are often times enlarged to assist with pushing and packing soil. Head-lift diggers possess enlarged keratinous nose pads (rhinarium) and rely on the use of these nose pads to move soil. Some species of *Spalax* also use their nose pads to thump their burrows and communicate using vibrations (Nevo et al., 1991). The rhinarium is strongly anchored to the nasals, and in the species with prominent nose pads, the nasals are widened and the premaxillae bow outwards (Fig. 5). Some mylagaulid rodents from the mid Miocene may have possessed such nose pads, but some coeval mylagauline mylagaulids are the only known rodents that bore horns on their skulls (see Figure 1E_1, E_2; e.g., Hopkins, 2005; Czaplewski, 2012). Four species of *Ceratogaulus* and one species of *Mylagaulus* possessed paired, bony horns, the function of which have been variously interpreted (summarized in

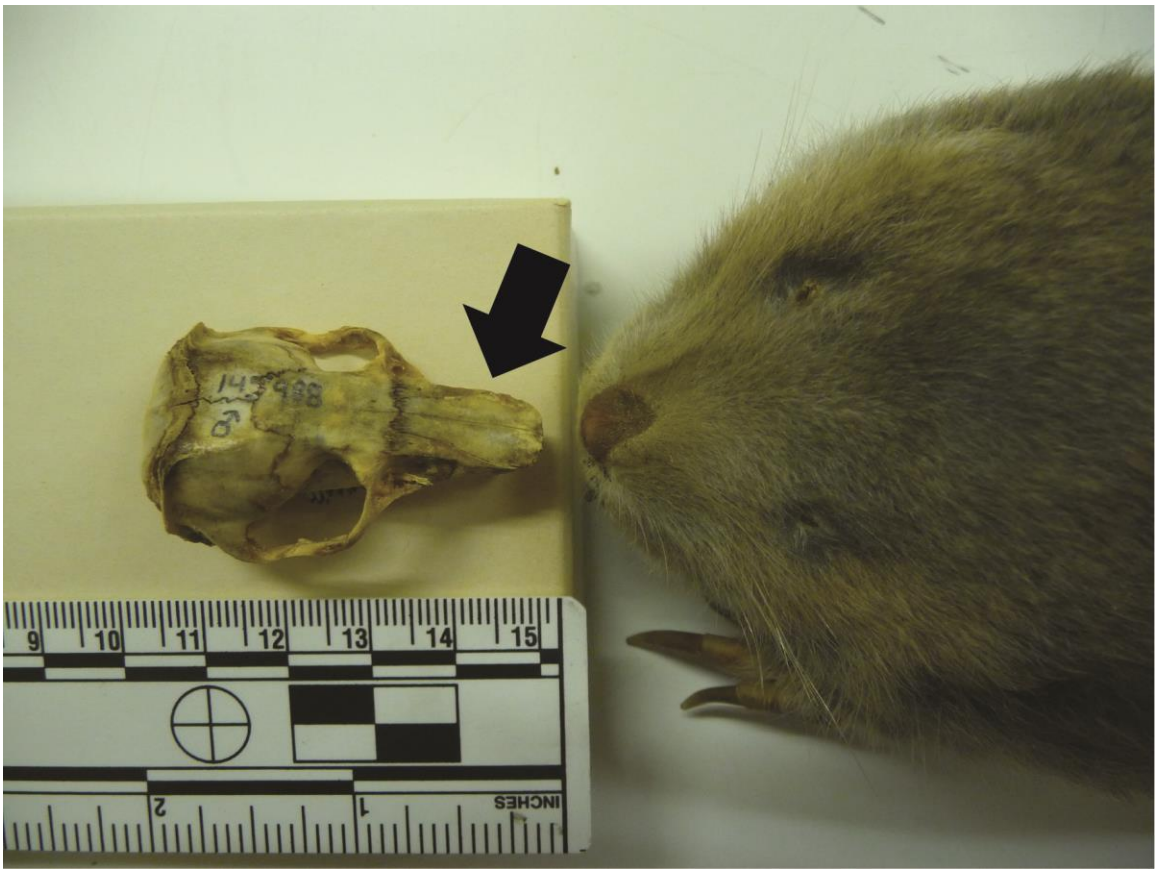

Figure 5—Skull and skin of *Myospalax myospalax* (KU 145988) demonstrating the rhinarium covering the nose and the structure of the nasal bones beneath. The nasals are elongated and widened (arrow) such that the external incisors are not visible in dorsal view. The nasals are also somewhat rugose to accommodate the attachment of the rhinarium.

Hopkins, 2005), although their use for burrowing (Gidley, 1907; Fagan, 1960) and defense against predation (Hopkins, 2005) are the most preferred hypotheses. The likelihood that some euhapsines possessed nose pads and others possessed horns is explored in Chapters 2 and 5 using comparative functional anatomy, epi-illumination microscopy, and CT scanning.

What is essential to clarify is that while some of these characters (such as grooved incisors) may individually occur in epigeal taxa, the combination of these characters occur only

in burrowing taxa (e.g., Hildebrand, 1985; Korth and Rybcyznski, 2003; Samuels and Van Valkenburgh, 2009). The specific combination of characters—such as the association of procumbent incisors and elongate rostra in chisel-tooth diggers and widened zygoma and broadened occipitals in head-lift diggers—and amount of specialization of those characters (e.g., degree of occipital tilting or incisor procumbency) further specialize a species for a specific burrowing behavior. Though nearly all subterranean rodents have external incisors, for example, only chisel-tooth diggers have highly procumbent incisors as a consequence of their usage as the primary digging tools (e.g., Lessa, 1990; van der Merwe and Botha, 1998). Certain characters only occur in burrowing rodents—proodont incisors, diminished or absent eyes, and dramatically broadened occipital regions—and are never observed in epigeal rodents but evolve independently in burrowing lineages (Nevo, 1999). Some characters, such as high incisor procumbency and the presence of a capsular process on the mandible have been used as sufficient evidence for interpreting burrowing behavior in fossil organisms (Korth and Rybczysnki, 2003; Korth, 2007a,b). Distinguishing epigeal and burrowing rodents from truly subterranean rodents is possible based on the functional morphology presented herein (compare figure 9.2c of Nevo, 1999 to figure 9.2a,b,d–f). The mosaic occurrence of certain skull characters is outlined for the new species and genus described in Chapter 2, and the use of incisor characters to finely differentiate between morphotypes associated with specific burrowing behaviors is outlined in Chapter 4.

SUMMARY OF DISSERTATION

Chapter 1 (i.e., this chapter) is an overview of the dissertation. It summarizes the remaining chapters and provides an introduction to the systematics of Castoridae and the terminology used by ecologists and morphologists studying rodent burrowing behavior.

Chapter 2 contains the systematic revision of the tribe Euhapsini. It includes a description of a new species of the genus *Euhapsis*, the description of a new genus of euhapsine (*Paraeuhapsis*), and a phylogeny of the known representatives of the Euhapsini. The similarity of *Euhapsis* and *Paraeuhapsis* to modern subterranean rodents is assessed, and both the evolutionary patterns within the tribe and the convergent evolutionary patterns of subterranean rodents from the North American Oligocene and Miocene are discussed.

Chapter 3 is an investigation of the function of grooved incisors in burrowing taxa, testing multiple previously proposed hypotheses for their function. *Paraeuhapsis* bears a set of labial grooves in the enamel of its upper incisors. *Paraeuhapsis* and *Castoroides* are the only castorids that produced grooved incisor enamel. This character has a limited distribution among modern rodents and is certainly a convergent feature. Experiments on replica teeth were performed to determine compressive strength in grooved and grooveless replica incisors. A literature review of the dietary and burrowing preferences of those rodents with grooved incisors was used to determine if any correlation exists between grooved incisors and behavior.

Chapter 4 is an investigation of the incisor characters that correlate with burrowing behavior. This chapter consists of a survey of modern burrowing and subterranean rodents, and a correlation between incisor morphology and burrowing style is presented. This correlation is then applied to fossil subterranean rodents to interpret their lifestyles and to refine and compare with previously reported interpretations of fossil behavior.

Chapter 5 is a detailed study of the unique cranial musculature and integumentary structures of *Paraeuhapsis*. The size, position, origin, and insertion of the masticatory muscles and some of the rostral muscles were interpreted based on the occurrence of the muscle attachment sites on the skull. The modification of the nasal bones described in Chapter 2 prompted additional investigation, so additional materials and methods, such as epi-illumination microscopy and micro-CT scanning, were used to study the size, morphology, and internal structure of the nasal bones in order to provide insight on the nature of the integumentary structure attached to the nasals. A reconstruction of the soft tissues of the head is presented at the end of this chapter.

Chapter 6 ties together the findings of the preceding chapters to interpret the ecology and behavior of euhapsine beavers. Though there are currently no known burrows attributed to euhapsines, an attempt is made to speculate on the likely form of their burrows. A discussion of the evolution of North American climates and landscapes through the Oligocene and Miocene and how these parameters affected patterns of convergent evolution in extinct subterranean rodents is provided. Lastly, this dissertation provides a framework for the direction of ongoing research needed in this area of study.

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NEW FLAT-SKULLED BEAVERS OF THE NORTH AMERICAN LATE OLIGOCENE AND EARLY MIOCENE

SUMMARY

We here propose a new genus of euhapsine beavers, propose a new species in the genus *Euhapsis*, and discuss the paleoecology of the flat-skulled rodent tribe Euhapsini. The new species is a primitive euhapsine from South Dakota, characterized by a shallow skull that is nearly as wide as it is long. The previously known euhapsine beavers *E. breugerorum* and *E. ellicotae*, from the early Miocene of Wyoming and Nebraska, are redescribed as a new genus, *Paraeuhapsis*, separable from *Euhapsis* on the basis of a deeper, more dome-shaped skull and a shallow medial groove on the upper incisors. The euhapsine beavers were an Oligocene–Miocene radiation of subterranean beavers that co-evolved with the spread of grasslands during a period of cooling and drying, and may be one of the most highly specialized burrowing mammals. Adaptations that made them uniquely suited to burrowing include an occipital expansion of the mandibular fossa, a shortened rostrum, and procumbent incisors. The genus *Paraeuhapsis* is even further specialized for digging, and is characterized by a near elimination of the infraorbital foramen, loss of the massteric tubercle, and the presence of thick and rugose nasal bones that likely supported a keratinous nose pad or horn. *Paraeuhapsis* is characterized by a unique zygomasseteric system in which the masseter muscle is reduced, the temporalis muscle is emphasized, and the jaws occluded primarily in a dorsoventral motion rather than an anteroposterior motion. Euhapsines were likely adapted to shallow burrowing, sand swimming, and feeding on grasses, roots, and tubers, analogous to modern day geomyids and bathyergids.

INTRODUCTION

Martin (1987) recognized a clade of flat-skulled, short-nosed fossorial beavers as a tribe, Euhapsini. The euhapsine beavers are not only the most fossorially adapted beavers, they are also among the most fossorial rodents of all time, resembling the modern blesmols (Bathyergidae) and blind mole rats (Spalacidae, Spalacinae). Martin (1987) described two new species of *Euhapsis*, placing three species in *Euhapsis* and two in *Fossorcastor*. We here report a new species of *Euhapsis*. The significant morphologic differences between this new species and previously recognized species of *Euhapsis*, relating to the organization of cranial musculature which likely reflect differences in burrowing behavior, justifies the redescription of two previously recognized species of *Euhapsis* into a separate genus.

Tribe Euhapsini currently consists of two genera, *Euhapsis* and *Fossorcastor*, with four recognized species in the genus *Euhapsis—E. platyceps*, *E. breugerorum*, *E. ellicottae*, and *E. luskensis*. The holotype of this genus, *E. platyceps* (CM 1220), was described by Peterson (1905). Martin (1987) erected the tribe Euhapsini with his description of *E. breugerorum* and *E. ellicottae*. Since that time, the only new species of *Euhapsis* that has been recognized is *E. luskensis* (Xu, 1996). *E. platyceps* is characterized by having the broadest and flattest skull of the genus, whereas *E. luskensis* has the narrowest skull of the genus. *Fossorcastor* also possesses a shortened rostrum, but the skull is deeper than *Euhapsis* and lacks an expansion of the mandibular fossa into the occipital region (Martin, 1987). The members of this tribe, as well as the other palaeocastorines, have been interpreted as fossorial (Schultz, 1942; Martin, 1987; Korth, 2001; Rybczynski, 2007; Samuels and Van Valkenburgh, 2009), though only the remains

of *Palaeocastor* and *Pseudopalaeocastor* have been discovered *in situ* within burrows (e.g., Martin and Bennett, 1977).

Matthew and Gidley (1904) reported a beaver skull (AMNH 10818) from the "Rosebud Formation" of South Dakota. Macdonald (1963) considered the deposits that produced that specimen as equivalent to the Oligocene Monroe Creek Formation and that assignment is adopted here. Matthew and Gidley (1904) thought that the skull pertained to *Steneofiber pansus* Cope 1874 from the early late Miocene of New Mexico, but the convex upper incisor enamel of *Steneofiber* places it in the subfamily Castorinae (Rybczynski, 2007). Stirton (1935) placed almost all the beaver material from the Monroe Creek Formation described by Matthew (1907) into *Palaeocastor simplicidens* including AMNH 10818. Stirton (1935) further set *Steneofiber pansus* as the type species of a new genus, *Monosaulax,* explaining the designation of AMNH 10818 as *M. pansus* by Samuels and Van Valkenburgh (2009). The flattened enamel of the incisors, however, clearly places this specimen in the subfamily Palaeocastorinae (Martin, 1987). Although the flatness of the skull is striking, the specimen is covered by many small cracks, perhaps leading previous workers to suspect that crushing may be responsible for its unusual proportions. These cracks, however, are not accompanied by displacement and are not likely taphonomic. AMNH 10818 is remarkably shallow and flat, and the only other beaver to show these proportions is *Euhapsis platyceps*. AMNH 10818 also shares with *Euhapsis* an exceptionally short rostrum and a deep zygomatic arch—a feature noted by Matthew and Gidley (1904) —that is tilted inwards (nearly vertical in most other beavers). Both also display comparatively small orbits that are oriented upwards. The upper surface of the rostrum forms a flat surface extending back to the sagittal crest and is about the right size and shape to form the base of a keratinized structure of the sort seen in some spalacid rodents (Hildebrand, 1985). We

consider the new holotype less specialized than *E. platyceps*, probably representing the primitive condition.

Institutional Abbreviations—**AMNH** and **F:AM**, American Museum of Natural History, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh; **KUVP**, University of Kansas Natural History Museum and Biodiversity Institute, Vertebrate Paleontology, Lawrence.

METHODOLOGY

Length measurements were obtained using digital calipers with an accuracy of 0.01 mm. Dental measurements and nomenclature follow that of Stirton (1935). Phylogenetic analyses were conducted using TNT v1.1 (Goloboff et al., 2008). The character matrix was modified from Rybczynski (2007), with new and modified characters noted (Appendix I).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowditch, 1821

Superfamily CASTOROIDEA Gill, 1872

Family CASTORIDAE Gray, 1821

Subfamily PALAEOCASTORINAE Martin, 1987

Tribe Euhapsini Martin, 1987

PARAEUHAPSIS, gen. nov., Schmerge and Martin, 2015

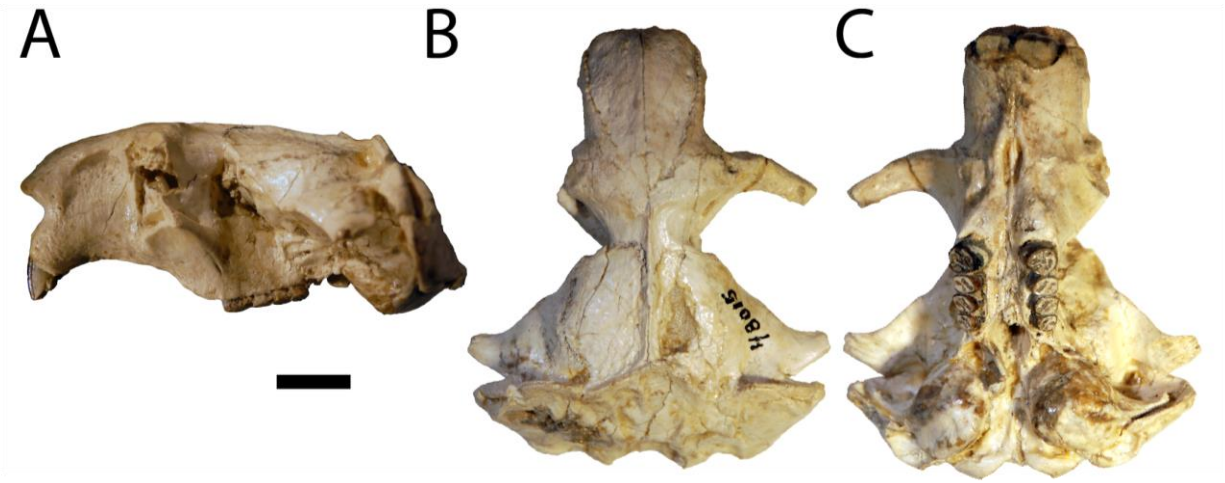

Figure 1—Skull of *Paraeuhapsis ellicottae*, gen. nov. (KUVP 48015) in lateral (A), dorsal (B), and ventral views (C). Scale bar 1 cm.

Type Species—*Paraeuhapsis ellicottae* Martin, 1987

Referred Species—*Paraeuhapsis breugerorum* Martin, 1987

Type locality and horizon—KUVP Coll.Loc.Wy-115, Niobrara County, Wyoming; Harrison Formation; early Miocene; latest Arikareean North American Land Mammal Age.

Etymology—For its similarity to *Euhapsis*.

Diagnosis—Rostrum short, skull flattened with the nasals rising slightly above the cranium, mandibular fossa extends into the occipital region, incisors grooved.

Description—Differs from *Euhapsis* in having a deeper skull with a larger and more elongated rostrum whose ventral surface slants upwards (Figs. 1–2). The incisors are more procumbent and the ventral surface of the rostrum is constricted along the incisive foramina (smooth in *Euhapsis*). The anterior zygomatic plate is shallower, smaller, and more inclined than in *Euhapsis*. The cranium is more rounded (extending dorsally above the zygomatic arch) and the zygomatic arch is well above the gum line, whereas it is near the gum line in *Euhapsis*. The nasal

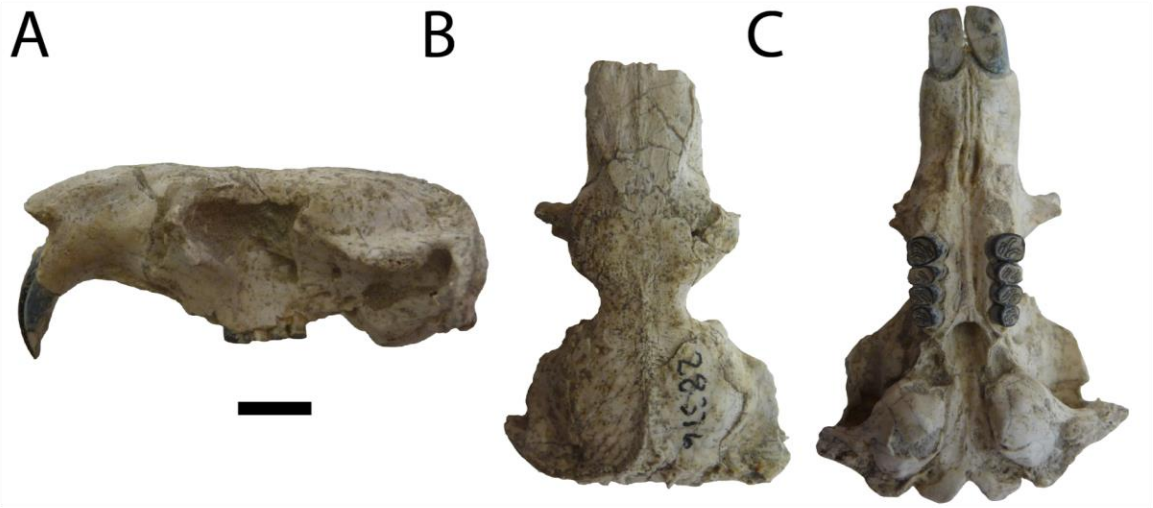

Figure 2—Skull of *Paraeuhapsis breugerorum*, gen. nov. (KUVP 28376) in lateral (A), dorsal (B), and ventral views (C). Scale bar 1 cm.

bones are elevated dorsally above the rest of the cranium. The massteric tubercle is absent, and other space for attachment of masseter muscles is completely eliminated from the rostrum. The masseter musculature clearly attaches to the zygomatic plate (protrogomorphy) rather than to the rostrum (sciuromorphy). The mandibular fossa is expanded caudally and laterally into the occipital region, where it terminates in a deep pocket. The articular condyle of the mandible fits tightly into this pocket, and this pocket clearly serves as a fixed point of articulation for the lower jaws. The upper incisors possess a single medial groove on the labial surface. The size of the cheek teeth decreases noticeably posteriorly. The occlusal surface of P4 is round.

The mandible of *Paraeuhapsis* is robustly constructed (Fig. 3). The coronoid process is tall and posteriorly curved. The articular process is medially deflected from the plane of the coronoid process. The angular process is laterally deflected from the mandibular body, and a pocket is created on the lateral and medial faces of its projection. A capsular process is present.

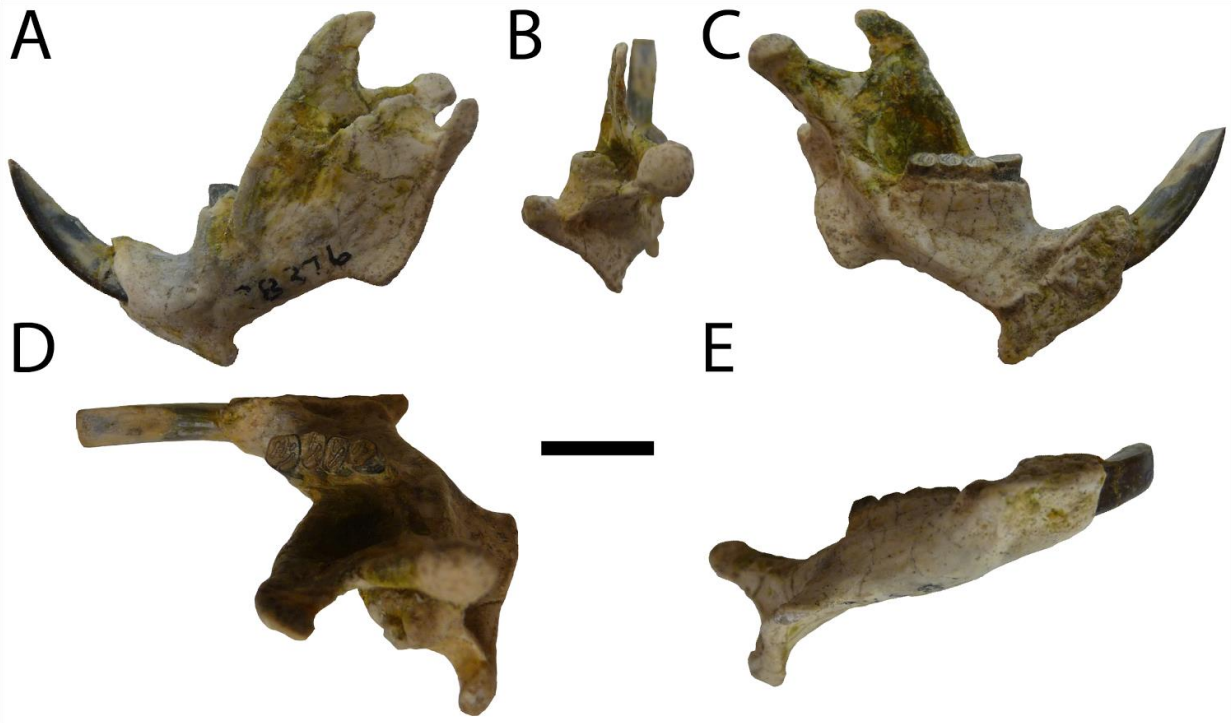

Figure 3—Left mandible of *Paraeuhapsis breugerorum*, gen. nov. (KUVP 28376) in lateral (A), posterior (B), medial (C), dorsal (D), and ventral views (E). Scale bar 1 cm.

The ascending ramus is separated from the toothrow by a deep pocket. The mandible of *Paraeuhapsis ellicottae* is unknown.

Discussion—As previously noted in the description of "*Euhapsis" ellicottae* and "*E." breugerorum* (Martin, 1987), their skulls differ in proportions from the genotypic species and resemble each other. With the description of an additional and more primitive species of *Euhapsis* that has the general skull proportions of the genotypic species, recognizing a new genus is appropriate to reflect the anatomical diversity exhibited in the known specimens. The functional and evolutionary significance of the masseter arrangement and the pocket formed posterior to the mandibular fossa is discussed herein.

Genus *Euhapsis* Peterson, 1905

Genotypic Species—*Euhapsis platyceps* Peterson, 1905

Amended Diagnosis—Broad, shallow skulls and short rostra. Superficial masseter posterior muscle originating behind ventral zygomatic apex; anterodorsal portion originating even with infraorbital foramen.

EUHAPSIS MARTINI, sp. nov., Schmerge 2015

Holotype—AMNH 10818, skull and mandible.

Type Locality and Horizon—Below Lake Creek, probably Bennett County, South Dakota (transcribed from a note with the specimen by T. M. Stout). Although the age of the specimen is not clearly indicated, it is most likely from beds equivalent to the upper Oligocene Monroe Creek Formation in Nebraska (Macdonald 1963).

Etymology—Named for the vertebrate paleontologist Larry D. Martin, who contributed significantly to the understanding of fossorial beavers and who passed away during the preparation of this report.

Diagnosis—Skull flat and broad, occiput vertical, incipient posterior expansion of the mandibular fossa, incisor enamel flattened, pocket on lateral surface of rostrum just anterior to zygomatic.

Description—The skull is nearly complete, with only the left zygomatic arch unexposed (Fig. 4). Descriptive measurements of the skull are in Table 1. The incisors are broken off near the eruption from the alveoli; all cheek teeth are present. The skull is flattened in proportion as in *E. platyceps*, but the skull is somewhat taller than *E. platyceps*. The rostrum is short as in other euhapsines. The pocket for lip retractor muscles is present on the rostrum anterior to the

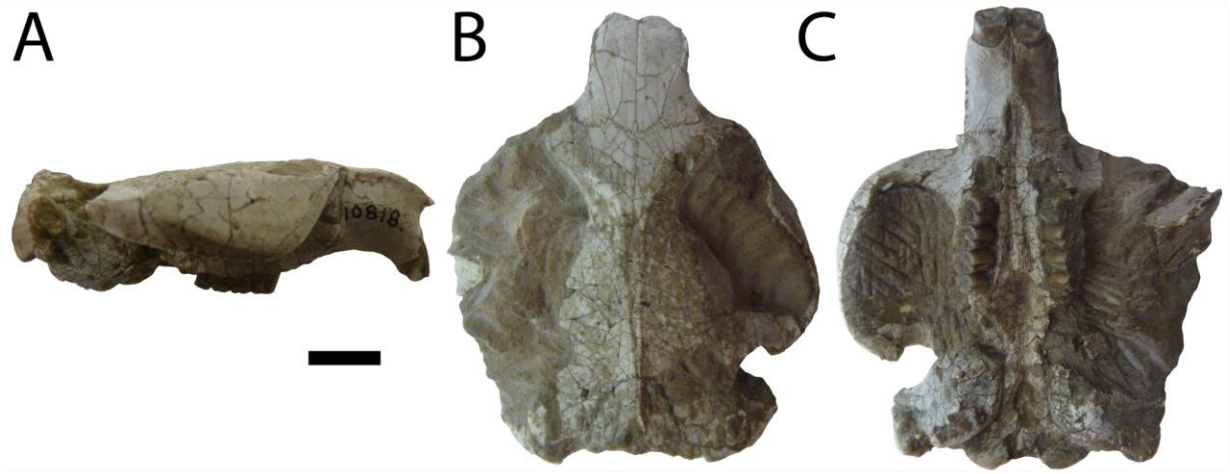

Figure 4—Skull of *Euhapsis martini*, sp. nov. (AMNH 10818) in lateral view (A), dorsal view (B), and ventral view (C). Scale bar 1 cm.

zygomatic arch, but they are shallower relative to the pits of *E. platyceps* and *Paraeuhapsis*. The nasals bend downward anteriorly, and are narrower and less rugose than *Paraeuhapsis*. The nasals of *Euhapsis* may generally be considered to be light in construction; the nasals of *E. martini* bear limited rugosity, as does *E. luskensis*. The nasals of *E. platyceps* are lost from the holotype. The nasals are elongate, and their anterior ends obscure the incisors in dorsal view. The nasals terminate in line with origination of the orbital margin. The orbits face dorsally, but are larger than other members of *Euhapsis*. There is a single sagittal crest that diverges at the interorbital constriction.

The zygoma are broadened into a zygomatic plate, as in most other castorids. The infraorbital foramina open in a plane immediately dorsal to the zygomatic plate, as opposed to opening slightly anterior to the zygomatic plate as in other castorids.

Skull length	57.04
Occipital condyle width	15.89
Rostrum length	18.00
Rostrum breadth	15.96
Interorbital breadth	10.82
Braincase breadth	23.30
Braincase height	14.92
Zygomatic breadth	49.55
Diastema length	18.90
Incisive foramen length	4.89
Bony palate length	18.12
Width of bony palate at first molar	2.78
Postpalatal length	22.64
Auditory bullae length (average)	13.285
Occiput angle (degrees)	88

Table 1—Cranial measurements of *Euhapsis martini*, sp. nov (AMNH 10818). Measurements in mm, except for occiput angle.

Many of the foramina utilized by Korth and Rybczynski (2003) and Rybczynski (2007) to identify character states are difficult to identify on AMNH 10818 due to the numerous cracks and the remaining matrix left on the specimen. The incisive foramina occur anterior to premaxillary-maxillary suture. The caudal ends of the incisive foramina are joined to the palatine foramina by two long, shallow grooves.

Euhapsis martini lacks an interparietal bone, which has been considered a synapomorphy of *Euhapsis* (Xu, 1996). The occiput is vertical, in contrast to the strongly forward tilted occiput of *E. platyceps* and *E. luskensis*. The external auditory meatus rises above the level of the zygomatic arch. The auditory bullae are flask shaped and not inflated. The mandibular fossa is elongate, but does not form a small socket as in all other euhapsines as a result of the vertical orientation of the occiput.

The upper cheek tooth pattern is P4–M3, as in all castorids more derived than *Agnotocastor* (Fig. 4–5). The tooth rows diverge caudally. M1 is approximately the same size as M2. The fossette pattern is similar for all of the upper cheek teeth. The parafossette is oriented at an angle to the sagittal plane in P4, but it is oriented perpendicular to the sagittal plane in M1–M3. The mesofossette is curved, and reaches the labial enamel surface in P4, M2, and M3 (i.e., a mesoflexus). The curvature approaches 90 degrees in P4 and M1, but is less than 30 degrees in both M2 and M3. In P4 and M1, the metafossette is separated from the mesofossette by a small

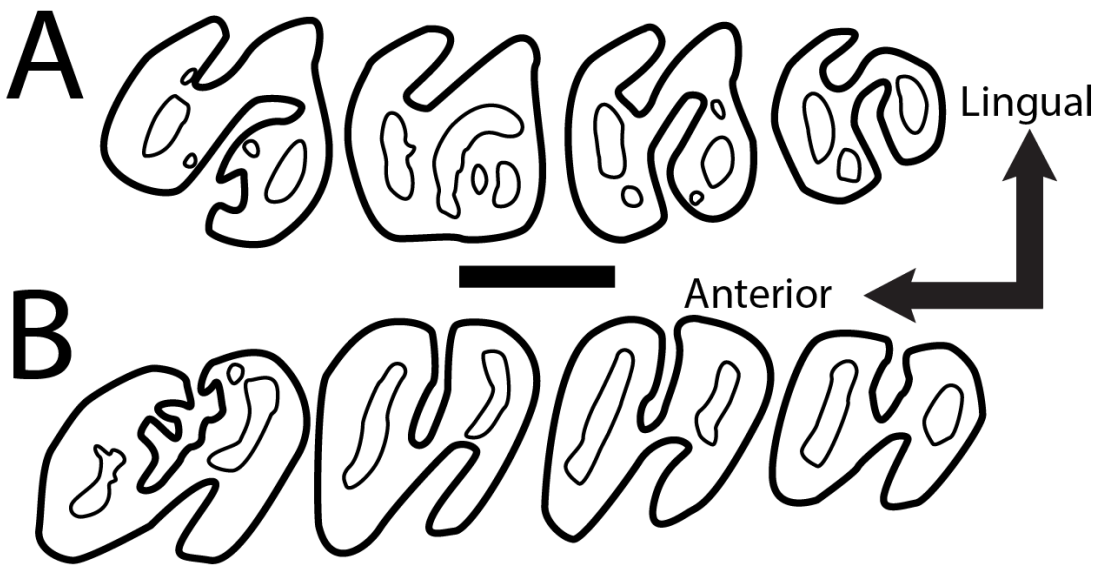

Figure 5— Upper dentition (A) and lower dentition (B) of *Euhapsis martini* sp. nov. (AMNH 10818). Scale bar 2 mm.

accessory fossette (it is attached to the mesofossette in P4). This smaller fossette is absent in M2 and M3. The hypoflexus is shortest in P4, covering less than 25% of the transverse width of the tooth. The hypoflexus opens to the outside margin of the enamel as in *E. luskensis* (upper molars not known from *E. platyceps*), similar to the condition seen in *Agnotocastor* and some other palaeocastorines. The molars are highly worn, as noted by Matthew and Gidley (1904). Tooth measurements are in Table 2.

Both mandibles are preserved, but are incomplete (Fig. 6). Both lower incisors are broken off right at their eruption from the alveoli. There is a deep pocket for the insertion of the deep masseter musculature. This pocket is the same as that of *Paraeuhapsis breugerorum*, and is similar to that of modern *Geomys*, but is both wider and deeper. The incisors are elongated as in other fossorial rodents that use their incisors for digging. The caudal end of the right incisor can be seen inside of the pocket for the masseter; there was likely a capsular process lying above this end as in other euhapsines and fossorial rodents. The coronoid processes of the mandible are broken, but the preserved portions of each rise to the height of the articular process, so they likely rose above the articular process when complete. The coronoid and articular processes occur in the same plane. The angular process lies only somewhat laterally to the articular condyle.

The cheek tooth pattern is p4–m3 (Figs. 5–6). The hypoflexid is arranged at an oblique angle, but the remaining fossettids are arranged nearly perpendicular to the sagittal plane. A mesoflexid is present on all lower cheek teeth. The parafossettid is shorter than the metafossettid in p4, but the metafossettid is longer in m1–m3. The fossetids are all elongate, except for the paraflexid of m3 which is subcircular.

	Left	Right
P4 length	3.28	3.24
P4 width	3.23	3.23
M1 length	2.97	2.94
M1 width	3.35	3.29
M2 length	3.00	2.95
M2 width	3.29	3.20
M3 length	2.31	2.39
M3 width	2.78	2.72
p4 length	3.40	3.44
p4 width	3.17	3.21
m1 length	3.42	3.55
m1 width	3.42	3.42
m2 length	3.08	3.07
m2 width	3.31	3.34
m3 length	2.70	2.82
m3 width	2.69	2.65

Table 2—Dental measurements of *Euhapsis martini*, sp. nov (AMNH 10818). Measurements in mm.

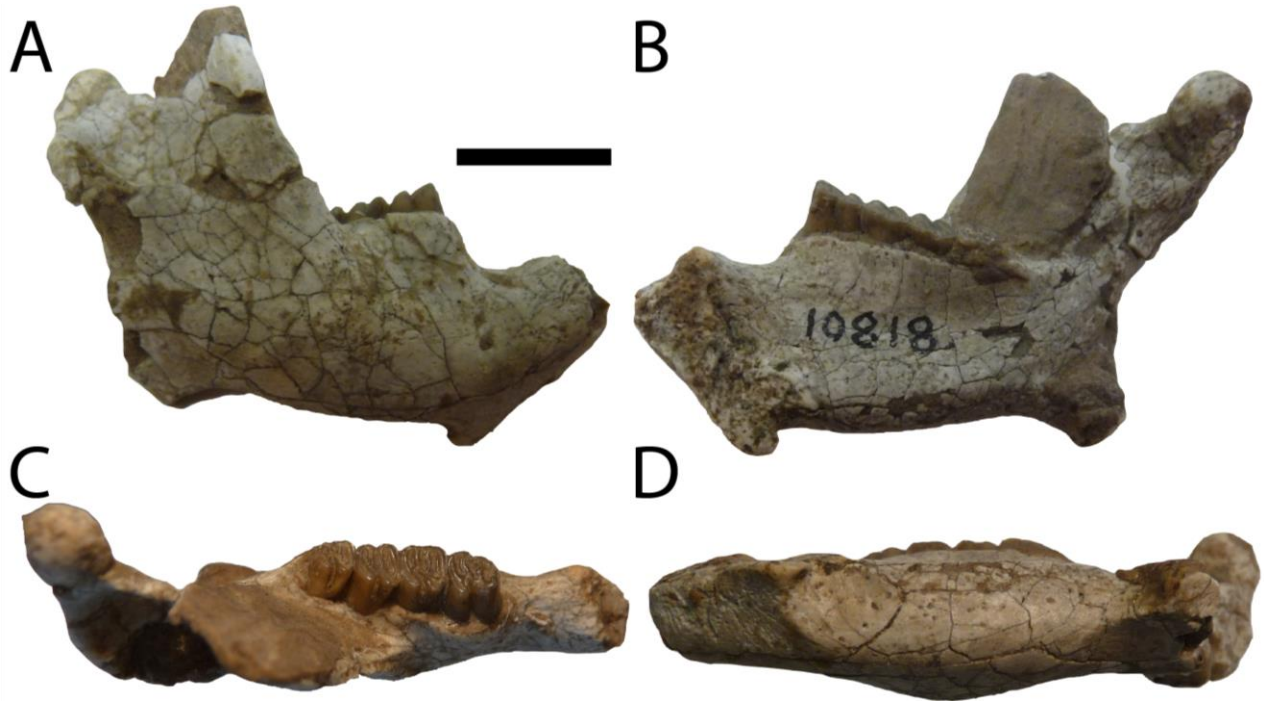

Figure 6—Right mandible of *Euhapsis martini*, sp. nov. (AMNH 10818) in lateral (A), medial (B), dorsal (C), and ventral views (D). Scale bar 5 mm.

Discussion—*Euhapsis martini* differs from the type species primarily in the more incipient nature of its characters. The rostral pocket, which is the defining character of the tribe Euhapsini, is present in *E. martini*, albeit much more shallowly by comparison to the other euhapsines. The vertical orientation of the occiput is reminiscent of the primitive palaeocastorine *Palaeocastor* cf. *nebrascensis*, whereas the occiput in all other euhapsines displays some degree of tilting. A progressive tilting forward of the occiput seems to be an evolutionary pattern in separate clades of euhapsine beavers, as primitive members of *Euhapsis*, *Paraeuhapsis*, and *Fossorcastor* all possess a nearly vertical occiput, whereas the derived members, particularly *E. platyceps*, possess strongly tilted occipital regions. The occiput of *F. greeni* is less tilted than that of *P. ellicottae* or *E. platyceps*, however, which in concert with the presence of occipital expansion of the mandibular fossa in *Euhapsis* and *Paraeuhapsis*, is evidence that *Fossorcastor* may have

utilized a burrowing strategy distinct from the other euhapsines. The forward tilting of the occiput is a key evolutionary step for the formation of the expanded pocket of the mandibular fossa that defines all derived euhapsines.

Comparison to the preserved left mandible of *P. breugerorum*, which Martin (1987) used to diagnose hystricognathy, demonstrates that the mandible of *E. martini* is clearly modified somewhat from the sciurognathous. All species of *Euhapsis* were only somewhat modified from sciurognathous condition, whereas the angular processes of *Paraeuhapsis* are strongly laterally deflected, creating additional space for attachment of the masseter musculature. Martin (1987) regarded the mandible of *P. breugerorum* as hystricognathous, but Xu (1996) and Korth (2001) referred to as it as a specialized case of sciurognathy. The nomenclatural and functional significance of this arrangement are addressed in more detail with the discussion of the zygomasseteric system.

AMNH 10818 has also been regarded as *Monosaulax pansus*. This can be shown to be incorrect based on a variety of characters. The flattened enamel of the incisors is a clear character of the palaeocastorine beavers rather than the Castorinae to which *Monosaulax* pertains (Martin, 1987). Peterson (1905) regarded the extreme width of the skull as a defining character of *Euhapsis*, so the width of the skull, as well as its extreme flatnesss, make this new assignment appropriate. The absence of the characteristic pocket in the occipital region should further regard this specimen as a primitive example of *Euhapsis*.

DISCUSSION

Zygomasseteric system

Rodents are traditionally split into four groups based on cranial morphology: protrogomorphs, sciuromorphs, myomorphs, and hystricomorphs. Protrogomorphy is the primitive rodent condition, in which the origin of the masseter muscle is restricted to the ventral surface of the zygomatic arch (Korth, 1994). In the other three groups, the infraorbital foramen is variously modified to accommodate the expansion of the masseter muscle onto the rostrum (Simpson, 1945)—it is narrow but somewhat enlarged in the sciuromorphs, it becomes keyhole shaped (enlarged towards the top, but narrow at the bottom) in the myomorphs, and is dramatically enlarged in the hystricomorphs. Only one group of extant rodents, the mountain beavers (Aplodontidae) bear the protrogomorphous condition. All members of the super family Aplodontoidea (Aplodontidae + Mylagaulidae) were protrogomorphous (Flynn and Jacobs, 2008). Some authors regard this as a secondary reacquisition of the primitive character (e.g., Druzinksky, 2010). The mountain beavers are a burrowing group, and the one modern species has only been observed to perform scratch-digging behavior (Hopkins, 2005). Some, however, postulate that mountain beavers may be head-lift diggers (Druzinksy, 2010) and their cranial morphology is consistent with head-lift burrowing (Samuels and Van Valkenburgh, 2009). Burrowing behavior has, however, also evolved in each of the other groups, and is represented in extant groups. Sciuromorphs may be the most prolific burrowers, including such prominent burrowers as pocket gophers (Geomyidae). Several myomorphs from the family Muridae are obligate burrowers, such as the Arvicolinae, the Myospalacinae, and the Spalacinae (Lacey et al., 2000). Hystricomorphs have notable examples of burrowers, including the Bathyergidae and Heterocephalidae (i.e., the naked mole rat, *Heterocephalus glaber*). Bathyergoids, however, have a highly reduced infraorbital foramen by comparison to other hystricomorphs, and they are regarded as possessing a unique zygomasseteric system (e.g., Cox and Faulkes, 2014).

Protrogomorphy may, therefore, be useful for burrowing rodents, as is evidenced by the independent reacquisition of protrogomorphy by aplodontids, euhapsines, and bathyergoids.

Euhapsines bear only some superficial similarity to modern groups. They instead appear to possess a mosaic of characters that appear in different modern groups. From the dorsal perspective, they compare well with the subfamily Spalacinae. Both possess a shortened rostrum, and the skull width is relatively great, albeit greater in euhapsines. Spalacines possess a dramatically enlarged infraorbital foramen and a low sagittal crest, however. Some spalacines, such as Nannospalax (*Spalax*) *leucodon*, possess a slight caudal expansion of the mandibular fossa, but the articular condyle of the mandible does not lock into this expansion as well in *S. leucodon* as it does in the derived euhapsines. Bathyergoids lack this expansion, and the only member (*Bathyergus suillus*) with gross similarity to euhapsines has a much longer rostrum and is a scratch digger. Geomyids also lack this pocket, and they are fully sciuromorphous. Only the primitive *Euhapsis martini* bears similarity to geomyids or *B. suillus*. Euhapsines are most similar to the mylagaulids. This similarity has been noted previously (Peterson, 1905; Martin, 1987; Martin and Naples, 2002).

The space available for the attachment of the superficial masseter muscle to the rostrum is severely limited in *Paraeuhapsis*. The infraorbital foramen is restricted and slitlike (sciuromorphous), but the superficial masseter attaches to outside of the zygomatic arch rather than through the infraorbital foramen, resulting in a protrogomorphous state similar to primitive rodents. Further rostral modifications include extreme shortening of the rostrum and an increase in the space available for lip retractor muscles. *Paraeuhapsis* would not have been able to move its jaws forward and backward (propalinal movement) as in other rodents based on the diminished size of the superficial masseter. The mandibular fossa, however, is elongated toward

the occiput, where it terminates in an expanded region that likely functioned as a socket for the lower jaw to lock in place. This unique style of articulation for rodents would, in concert with the expanded zone of attachment for the deep masseter and temporalis muscles along the mandible, allow *Paraeuhapsis* to close its jaws by moving the mandible upward rather than forward.

Paraeuhapsis ellicottae has a flat cheek tooth wear pattern. This is unusual, as the antero–posterior jaw occlusion caused by the laterally expanded mandibular fossa of rodents creates a convex wear pattern on the upper tooth row and a complimentary concave wear pattern on the lower tooth row. This is taken as evidence that *P. ellicottae* relied primarily on the posterior expansion of the mandibular fossa to act as the primary articulation point as it articulated its jaws. Primates and omnivorous bears, which are the only other mammals with both grinding cheek teeth and a fixed rather than gliding jaw articulation, also have a flattened wear pattern of the cheek teeth. This likely occurs as a result of the uniform application of wear-inducing stress from the entire tooth row occluding simultaneously, resulting from a bite from a fixed articulation point.

The modified jaw closing apparatus is also reflected in the comparably enlarged coronoid process. The coronoid serves as the attachment for the temporalis muscle. The coronoid process is reduced in most rodents as the masseter is emphasized and the temporalis is reduced (Korth, 1994). The enlargement of the coronoid, and therefore the temporalis muscle, likely occurred to compensate for the reduction of the masseter mass.

There is considerable evidence that the masseter musculature is rearranged in euhapsines, particularly *Paraeuhapsis*. The enlarged fossae on the rostrum for the lip retractor muscles would have diminished the room for the attachment of the masseter. The infraorbital foramen and masseteric tubercle are shifted to the caudal end of the rostrum in *Fossorcastor* and *Euhapsis*,

and the masseteric tubercle is absent in *Paraeuhapsis*. The modification of the mandible in Paraeuhapsis, including the lateral deflection of the angular process, allows an increase in the size of the medial masseter. Protrogomorphy is the primitive rodent condition, in which the masseter origin is restricted to the zygoma. The condition present in *Paraeuhapsis* is clearly unique from true protrogomorphs (i.e., *Paramys*), but is justifiably utilized in describing the masseter arrangement of *Paraeuhapsis*.

The advantage of the rodent specialization of the masseter muscle mass has been to facilitate and increase the mechanical advantage generated by anteroposterior motion of the mandible. The three derived rodent cranial morphotypes (sciuromorph, myomorph, and hystricomorph) each derive their own unique mechanical advantage (Cox et al., 2012). The primitive condition (protrogomorphy) is derived from the primitive mammalian condition in which the jaw closes upward against the cranium rather than grinding laterally. This condition exists in insectivorous mammals, which are agreed to be the primitive mammalian condition, and carnivorous mammals. The advantage to a secondary reacquisition of the primitive protrogomorphic condition, therefore, is to increase the mechanical advantage of upward closure of the jaw.

Burrowing rodents can benefit from this system for any number of reasons. Head-lift digging, a behavior that is interpreted for nearly all euhapsines (Samuels and Van Valkenburgh, 2009), requires the skull to be strongly anchored to the soil column while strong actions of the neck muscles break away portions of the soil (Airoldi et al., 1976; Wake, 1993; Stein, 2000). A strong dorso–ventral bite force would accomplish this much better than a bite force oriented in the antero–posterior direction. Chisel-digging taxa, however, are more effective at burrowing by scraping their procumbent lower incisors against the (hard) soil with an antero–posterior motion

(Jarvis and Sale, 1971; Wake, 1993; Stein, 2000). Many geophytes (e.g., tubers) possess tough exteriors and soft interiors. In order to process these, a strong upward motion of the jaws is needed to remove a portion of the geophytes, but a strong lateral motion to grind the geophyte into digestible portions (such as that needed for seeds or grass) is not necessary. Reduction of the muscle mass of the skull may also play a role in streamlining an organism for burrowing. Bathyergoid rodents are derived from hystricomorphous ancestors, but the bathyergoid skull lacks the dramatically enlarged infraorbital foramen that characterizes hystricomorphs. Burrowing rodents tend to have fusiform bodies because the body is adapted to be the same diameter as the skull, which is the limiting size factor of burrowing rodents (Stein, 2000). A more efficient body shape can, therefore, be accomplished in chisel-digging taxa by diminishing the width of the skull and reducing the masseter mass, whereas a more efficient shape in head-lifting taxa can be accomplished by increasing the skull width.

The interpretation of hystricognathy in fossil rodents is contentious (e.g., Matthew, 1910; Wood, 1975; Korth, 1984; Wilson, 1986; Hautier et al., 2011). Korth (1994) regarded all castorids as sciuromorphous. Xu (1996) and Korth (2001) demonstrated that there is diversity of form in castorid mandibles. Rather than true hystricognathy, Korth (2001) defined the shape of the posterior aspect of the mandible as having a 'zig-zag' shape. Martin (1987) rather interpreted the mandible of *Euhapsis* as hystricognathous. A lateral expansion of the mandible, which is traditionally coined as hystricognathy (Korth, 1994), has clearly evolved numerous times, and what is clear in euhapsines is that the mandible has expanded to accommodate a shift of masseter musculature. Unambiguous hystricognaths, such as *Bathyergus suillus*, have a dorsoventrally flaring mandibular flange, whereas the expanded flange of euhapsines is primarly expanded ventrally and posteriorly. The mandibular configuration seen in *Paraeuhapsis* is highly similar to

that seen in other modern subterranean forms, such as *Geomys* or *Nannospalax*. This morphology is also reminiscent of the expansion of the masseter insertion in felids (i.e., modern lions), which appears to be in accordance with the expansion of the temporalis musculature that closes the jaw upward.

Cranial adaptations for burrowing

There are several recognized cranial characters that are associated with specialized digging behaviors in rodents (e.g., Nevo, 1979, 1999; Hildebrand, 1985; Stein, 2000; Samuels and Van Valkenburgh, 2009), and euhapsine beavers (Martin, 1987) are likely the most fossorially adapted rodents by virtue of possessing most of these characters (Table 3). Euhapsine beavers possessed small, upward-looking eyes, highly diminished external pinnae, and short limbs. Euhapsines were likely blind (due to upward-looking eyes and small orbits), but possessed enlarged lacrimal foramina. Most bathyergoids are blind, but use their eyes as to sense pressure changes and wind in their burrows in order to detect incursions into their burrow networks (Eloff, 1958). The lacrimal gland is utilized to moisten the eyes for this purpose.

Skull morphometric analysis has been utilized to determine the relationship between skull shape and burrowing behavior in rodents. Analysis of the skulls of bathyergid rodents determined that the upper incisors are more procumbent in chisel-tooth digging species than those that utilize a scratch-digging strategy (van der Merwe and Botha, 1998). They further found that chisel-tooth diggers had as much as 10% more enamel on their incisors relative to the scratch diggers. Samuels and Van Valkenburgh (2009) examined the shape of 318 skulls from 79 modern rodents from various families and 20 extinct species of castorids. They found two

Adpatation	Usage	Associated Burrowing	Modern Analog	Selected References
Flattened skull	Earth moving	Head lift	*Nannospalax*	Nevo et al. (1991)
Domed/tall skull	Distributes forces through skull from teeth	Chisel tooth, Head lift	*Cryptomys* (*Fukomys*)	Samuels and Van Valkenburgh (2009)
Pinched rostrum	Placement of lip retractor muscles	Chisel tooth, Scratch	*Geomys*	Stein (2000)
Keratinous nasal structure	Loosening earth and moving earth during excavation	Head lift	*Nannospalax*	Nevo (1999)
Wide zygomatic breadth	Increased space for masseter attachment	Head lift, Chisel tooth	*Nannospalax*	Hildebrand (1985)
Increase of squamosal size; decrease/absence of interparietal	Increase space of attachment for temporalis	Chisel tooth, Head lift	*Rhizomys*	Stein (2000)
Occiput widened and angled forward	Enables head to be tilted backward; increases space for rhomboideus attachment	Head lift	*Nannospalax*	Hildebrand (1985)
Increased height of sagittal and nuchal crests	Increases space for temporalis and rhomboideus attachments	Head lift	*Nannospalax*	Hildebrand (1985)
Proodont incisors	External teeth used for digging Food obtainment	Chisel tooth, Head lift; Scratch, Head lift	*Heterocephalus*, *Arvicola; Bathyergus*, *Geomys*	Wake (1993) Stein (2000)
Increased incisor enamel	Increases strength of teeth for digging	Chisel tooth	*Cryptomys* (*Fukomys*)	van der Merwe and Botha (1998)
Grooved incisors	Creates serrated edge for plant processing	Scratch, Head lift	*Geomys*; *Bathyergus*	Stein (2000)
Elongation of incisor socket	Increases tooth volume to compensate for wear	all	*Georychus*; *Geomys*	Lessa and Thaeler (1989)
Protrogomorphy	Improves dorso-ventral bite force	Head lift, Chisel tooth	*Aplodontia*; *Heterocephalus*	Druzinksy (2010)
Elongation of mandibular fossa	Improves dorso-ventral bite efficiency	Chisel tooth, Head lift	*Nannospalax*	Krapp (1965)
Reduced or lost eyes	Diminished need for sight below ground	all	*Nannospalax*	Stein (2000)
Enlarged lacrimal glands	Prevents eyes from drying out in subterannean settings Allows eye membranes to detect air pressure changes	all	*Nannospalax*	Eloff (1958)
Inflated auditory bullae	Increased ability to hear low frequency sounds below ground	all	*Nannospalax*	Stein (2000)
Reduced auditory meatus	Correlated with reduction of external pinnae to streamline the shape of the head	all	*Nannospalax*	Stein (2000)
Capsular process	Accomodates enlarged lower incisors	all	*Geomys*, *Heterocephalus*, *Nannospalax*	Stein (2000)
Hypsodont teeth	Offsets increased wear from soil ingestion and consumption of geophytes	all	*Arvicola*, *Ellobius*	Agrawal (1967)

Table 3—List of cranial characters associated with burrowing behavior in fossorial rodents.

primary factors that determine burrowing behavior: (1) whether the skull is long and flat (head-lift digging) or short and tall (scratch digging), with chisel-tooth digging lying somewhere between, and (2) whether the skull contained long, procumbent incisors (chisel-tooth digging) and an elongated mandibular fossa or short and nearly recurved incisors (scratch digging and head-lift digging). Skull morphometric analysis demonstrates that different species of euhapsines used chisel-tooth digging or head-lift digging behavior (Samuels and Van Valkennurgh, 2009).

Samuels and Van Valkennurgh (2009) evaluated the cranial morphology of rodents and found three morphospaces that the three rodent burrowing strategies occupy. Interestingly, all euhapsine beavers save for *Paraeuhapsis ellicottae* fall outside these well-defined morphospaces. There could be several explanations for this phenomenon. They could be transitional to these different derived strategies. They could have their own unique morphology that is outside the range of observed modern rodents, while still utilizing one of the three modern strategies. Or they could have their own unique burrowing behavior, a hypothesis that cannot be tested until an individual euhapsine is discovered inside a burrow.

The occiput is angled forward in many euhapsines. This modification allows for a wider range of motion of the head and permitted extra muscle attachments from the atlas and axis, which likely enabled the organism to use its head as a shovel to move loose sediment, as do modern spalacines (Watson, 1961). The highly shortened rostrum of these organisms is further evidence of this behavior, as a shortened rostrum is advantageous for pushing soil (Nevo, 1999). The skull of most euhapsines is shallow with a highly angled occiput. *Euhapsis martini*, however, has a shallow skull with a vertical occiput, whereas *Paraeuhapsis* has a much taller skull with degree of occipital tilting variable among species. These two genera obviously used two different burrowing strategies. *Euhapsis martini* may have been only incipiently adapted to

head-lift digging and may have supplemented with scratch-digging behavior, whereas *Paraeuhapsis* was an obligate head-lift digger.

A defining feature of many euhapsines is the presence of a secondary glenoid in the occipital region formed by the posterior expansion of the mandibular fossa. This feature was clearly used as an additional articulation point for the jaw. Some specimens can be seen with the articular process of the lower jaw clearly fixed in this pocket (Fig. 7). Whether this would have been the resting position of the jaw, or if taphonomic processes slid the jaw into this position, is

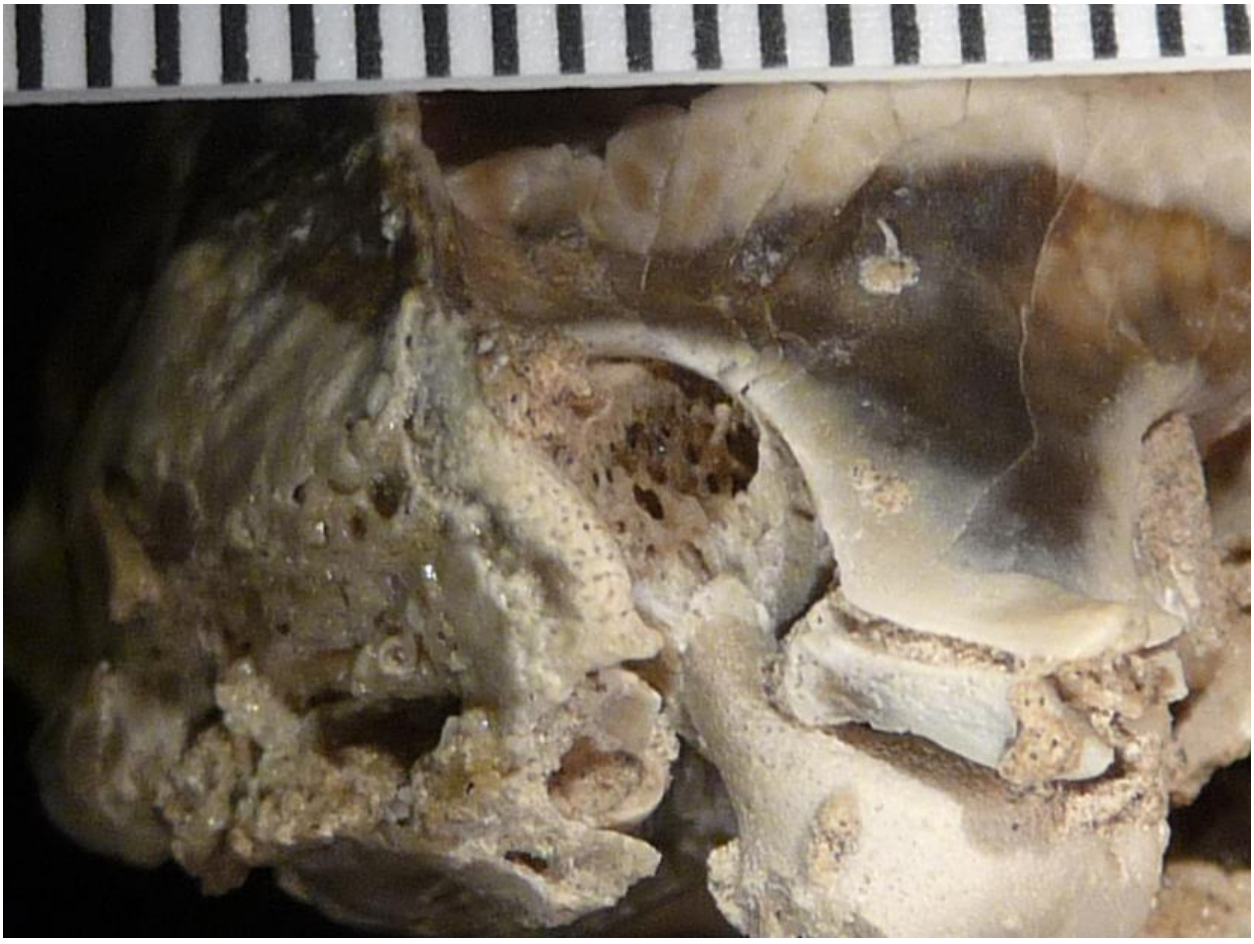

Figure 7—Close-up view of *Euhapsis luskensis* (F:AM 64589) showing the secondary glenoid formed by the caudal expansion of the mandibular fossa with the articular process of the mandible fixed inside of it.

not possible to assess. This feature is absent in *Fossorcastor* and *Euhapsis martini*, but is present in all other species of *Euhapsis* and *Paraeuhapsis*.

The presence of the medial, labial groove on the upper incisors of *Paraeuhapsis* is significant. This groove is absent in all other euhapsines, making this a useful diagnostic character for the group. There are several modern rodent taxa that have independently acquired such a groove, including the bathyergid *Bathyergus suillus* and the geomyid *Geomys*. There has been much speculation on the function of such a groove. Stein (2000) summarized the debate, suggesting that the three primary roles such a groove might play are: (1) easing the extraction of the teeth from the soil, (2) easing the collection of food material from the teeth, or (3) increasing the strength of the teeth. The third hypothesis is the most favored, but faces one potential set back in the fact that neither *Bathyergus suillus* nor *Geomys* use its teeth for burrowing. The argument could be made that due to the size of *B. suillus*, the grooves are a necessary structural element to counteract the forces placed on its teeth due to foraging for geophytes. The incisors of *Castoroides* (giant Pleistocene beaver) and *Hydrochoerus* (capybara) have numerous grooves on their incisors that have been argued to contribute to the overall strength of the teeth, similar to corrugation in cardboard or I-beams (Akersten, 1973). Another unconsidered possibility is that the presence of the groove changes the wear pattern of the teeth. The occlusal ends of the incisors are not present in KUVP 48015 or KUVP 48016, but examination of a specimen of *B. suillus* demonstrates a V-shaped notch following the groove at the occlusion surface. This wear pattern may be utilized to increase the efficiency of foraging, thus explaining its presence in taxa that are not chisel-tooth diggers.

Martin (1987) raised the possibility that the genus *Euhapsis* may have possessed a keratinized nose pad (rhinarium) or horn supported by the nasal bones. Rhinaria occur in many

burrowing mammals, including spalacids and golden moles (personal observation; Nevo, 1999). Given the redescription we propose herein, the genus *Euhapsis* itself did not have horn due to the relative fragility and smoothness of the nasal bones by comparison to *Paraeuhapsis*, though the presence of a rhinarium in *Euhapsis* is likely given its association with head-lift digging behavior. *Paraeuhapsis ellicottae*, as noted by Martin (1987), must have had fast-growing tissue covering the nasal bones due to the high number of nutritive foramina covering their surface. The nasals of spalacids appear to have some openings for increased blood supply and are elongated and thickened relative to other burrowing rodents. The nasals of *Paraeuhapis* are dramatically thickened, very noticeably rugose, and bowed upward. This condition is similar to that found in horned rhinoceros (Hieronymus et al., 2006), so the presence of a keratinzed horn in *Paraeuhapsis* is a possibility that requires further consideration.

Evolutionary patterns of specialized Miocene burrowers

Previous considerations of the relationships of the euhapsines have been limited to other systematic revisions of the tribe. Martin (1987) established the tribe when he recognized the genus *Fossorcastor* was related to *Euhapsis*. Xu (1996) proposed that the euhapsines were paraphyletic and should include the genus *Capatanka* and *Nannasfiber* to form a monophyletic clade. This further had the consequence of uniting *Fossorcastor* with castorines based on superficial similarity of their mandible structures. *Nannasfiber* has since been synonymized with genus *Pseudopalaeocastor* (Korth, 2001), who preferred the scheme of Martin (1987). Rybczynski (2007) recovered Euhapsini as a monophyletic clade, but only considered *Paraeuhapsis breugerorum*, *P. ellicottae*, and *F. greeni* in the analysis.

A phylogenetic analysis of the euhapsines is presented in Figure 8. Euhapsini is indeed a monophyletic clade. The genus *Steneofiber* pertains to the subfamily Castorinae, whereas *E. martini* is clearly nested with the Euhapsini. Each genus of euhapsines displays progressive tilting forward of the occiput from early late Arikareean to the late Arikareean, indicating that each genus independently acquired this character as an adaptation for burrowing. Only the genus *Paraeuhapsis* obtained the extreme specializations of the zygomassertic system resulting in a protrogomoprhic state, but *Fossorcastor* and *Euhapsis* display slight modifications to the rostrum and infraorbital foramen that were necessary for the transition from sciuromorphy to protrogomorphy.

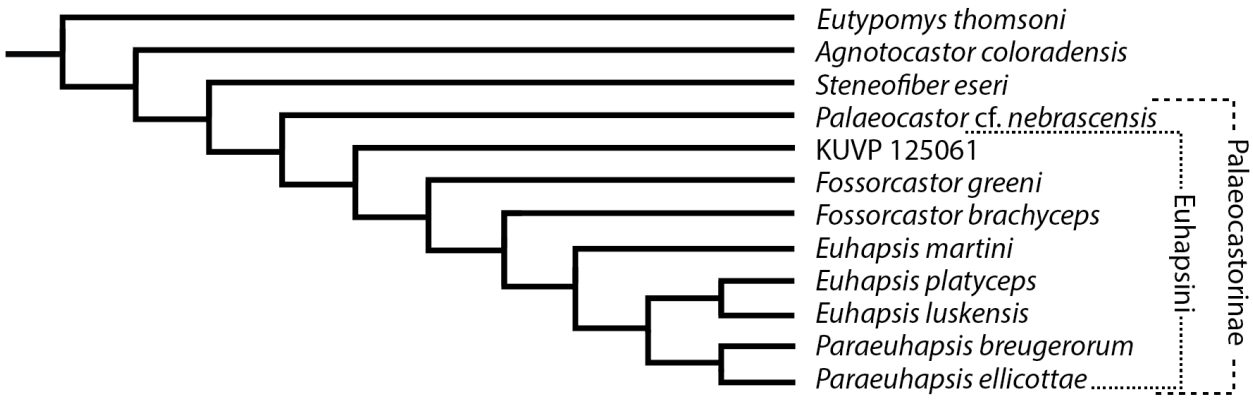

Figure 8—Phylogeny of Tribe Euhapsini.

Martin and Meehan (2005) demonstrated that repeated, extreme convergence of form (ecomorphy) in mammalian body plans could be explained by orbitally-mediated climate cycles (i.e., Milankovitch Cycles). The most spectacular case of this is the repeated evolution of saber-toothed feliforms in independent lineages, but this pattern has also been demonstrated for herbivore, shrew, and fossorial rodent ecomorphs. The euhapsine beavers were likely the first group of rodents to occupy the niche of head-lift-digging rodents in the late Oligocene and early

Miocene in North America, but they were succeeded later on by the mylagaulids in the middle Miocene (Hopkins, 2005). The Geomyidae had a large radiation during the late Miocene (Korth, 1994), and are presently the only chisel-tooth digging rodents in North America (Lacey et al., 2000). The Mylagaulidae were specialized for burrowing; most mylagaulids display a forward-angled occiput, and one of the lineages resulted in 5 species characterized by bony horns on the rostrum (Hopkins, 2005; Czaplewski, 2012). If *Paraeuhapsis* also possessed a rostral horn, the horned rodent ecomorph may be the terminal member of a cycle as was the case for dirk-toothed feliforms (Martin and Meehan, 2005). Chisel-tooth digging (Jarvis and Sale, 1971) and increased enamel strength (Nevo, 1999) correspond with increased soil hardness. Horns may have been an adaptation for digging (Gidley, 1907; Fagan, 1960), and since head-lift diggers typically dwell in softer soils (e.g., loess, Nevo, 1961), horns may have evolved for burrowing in very hard soils. The absence of horned rodents after the extinction of the mylagaulids may, therefore, potentially relate to the success and permanent establishment of grasslands in the North American interior. Hopkins (2005) suggested that the horns in mylagaulids were not useful for burrowing, and likely were used for defense instead. A defensive function is a reasonable interpretation for their use, if mylagaulid horns originally evolved in the context of fossorial behavior and were not useful for digging in the comparatively loose soils of the late Miocene and Pliocene. There remains the possibility also that there are other horned rodents that have yet to be discovered.

CONCLUSIONS

The description of the most primitively known beaver of the tribe Euhapsini warrants a systematic revision of the genus *Euhapsis*. *Euhapsis martini* is a palaeocastorine beaver that displays features consistent with its interpretation as the most primitive member of the tribe

Euhapsini. *Paraeuhapsis*, while closely related to *Euhapsis*, developed a unique zygomasseteric system and jaw closing apparatus unknown in any other type of rodent. The unique mosaic of characters found in *Paraeuhapsis* warrant separation into its own genus. *Paraeuhapsis* is one of the most adapted rodents for burrowing, but many of its adaptations still need to be evaluated in a functional context. While previous studies have certainly documented the gross behavior of this genus, much work remains to interpret the functional biology of this unique taxon.

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CRITICAL EVALUATION OF THE FUNCTION OF LABIAL GROOVES FOUND ON SOME UPPER RODENT INCISORS

SUMMARY

Function of labial grooves in the upper incisors of certain rodents is investigated both experimentally and with a literature review. Labial grooves in incisors form as a result of the infolding of the enamel. Upper incisor grooves are documented in 61 extant genera. Compression experiments were conducted with replica teeth cast from the extant bathyergid rodent *Bathyergus suillus* to test the hypothesis that rodents evolve these vertical grooves to strengthen the teeth. A literature review of diets of extant rodents with grooved incisors and other extant subterranean rodents was conducted to test the hypothesis that the groove plays a role in food acquisition. Grooves have no correlation with chisel-tooth digging behavior, and are likely a detriment to that behavior. Incisor grooves correlate most strongly with taxa that consume grasses and other geophytes. The hypothesis that grooves function as an aid in the release of the incisors from the soil or food objects was investigated based on interpretation of the incisor wear, examination of replica incisors, and comparison to grooves in man-made objects (forged blades and I-beams), but cannot be rejected. The incisors of some burrowing rodents are the primary burrowing tools, so the interpretation of the function of the grooves will help to disentangle their function from other behaviors in burrowing taxa. The results of these experiments are used to interpret the burrowing behavior and feeding ecology of the extinct euhapsine beaver *Paraeuhapsis* and the mylagaulid *Ceratogaulus*, both of which possess labial incisor grooves and were likely subterranean specialists.

INTRODUCTION

Complex tooth crowns are one of the characters that define mammals, with the morphology of the cheek teeth in particular serving as the hallmark for establishing relationships and functional anatomy in mammals (Feldhammer et al. 2007). Less well studied has been the morphology of the crowns of incisor teeth. This may be because the occlusal surface of most incisors is relatively simple by comparison to the occlusal surface of cheek teeth by virtue of absence of the numerous cusps that define the premolars and molars. The labial surface of many rodent incisors is in some ways as complex if not more complex than the cheek teeth crowns of other mammals. The various patterns of enamel growth in rodent incisors—uniserial, biserial, multiserial, pauciserial—have received much attention from workers investigating its functional, taxonomic, and phylogenetic significance (e.g., Martin 1997). Some researchers have even gone so far as to suggest that the labial surface of rodent incisors is homologous with the cheek teeth occlusal surface (Tummers et al. 2007; Tummers and Thesleff 2008; Ohazama et al. 2010). Several different groups of rodents independently developed longitudinal grooves in the upper incisor enamel, and these grooves have been useful in establishing the taxonomy of the family Geomyidae (e.g., Merriam 1895). The goal of this paper is to use the African bathyergid rodent *Bathyergus suillus* to interpret the function of grooved incisors in controlling diet and tooth strength.

Incisors have many functions. They are primarily used as a means of food acquisition, though they are not used in mastication. Incisors have a variety of morphologies to this end. Insectivorous mammals use their incisors as insect traps; the teeth are used to grasp insects which are then moved to the cheek teeth for mastication (e.g., Churchfield 1990). Carnivorans

evolved caniform incisors to assist in grappling with struggling prey (e.g., Mech 1970). Proboscidean incisors evolved into tusks for use in bark stripping and snow clearing (e.g., Lambert and Shoshani 1998; Putshkov 2003). Many omnivorous mammals (including hominids) have spatulate incisors that function to scoop food more effectively into the oral cavity (e.g., Fleagle 2013). In some mammals, incisors are used in grooming behavior, and they can sometimes take on tremendously derived forms to accommodate this function, such as the comb-shaped incisors of lemurs (e.g., Fleagle 2013). Incisors (and some additional teeth) are used for communication in many groups; nearly all mammals will display the incisors as a means to communicate threat potential, but such groups as equids, canids, and primates have evolved complex communication patterns that involve the incisors (e.g., Mech 1970; MacClintock 1976; Parr and Waller 2006). Finally, and most pertinent to this paper, incisors are also useful in some groups of rodents for soil excavation during burrowing (Hildebrand 1985).

Three primary hypotheses have been advanced to explain the function of the incisor groove in burrowing rodents. 1) The presence of a groove alters the wear pattern of the incisor and is hypothesized to function primarily to create a cutting edge useful in either food acquisition or burrowing (Merriam 1895). 2) The groove has also been hypothesized to serve as a fold in the enamel used to strengthen the incisor, similar to structure of an I-beam or corrugated steel (Akersten 1973). 3) The groove has been hypothesized to function as a means by which rodents can more easily extract their teeth from the soil or geophytes (which have tough exteriors) while burrowing (Russell 1968). The extraction hypothesis (hypothesis 3) will not be formally considered here, but the purpose of this study is to critically evaluate these hypotheses using experimental studies on the strength of replica incisors and a literature review of the diet of various rodents.

MATERIALS AND METHODS

To test the hypothesis that grooved incisors are stronger than grooveless incisors, compression tests were performed on replica incisors. The incisors of a cape dune mole rat (*Bathyergus suillus*; KU 79414) were molded in GT Products © 5092 high-performance mold making silicon. *Bathyergus suillus* was selected for study because its incisors are large compared to the incisors of other burrowing rodents and because no interpretation has yet been made for the groove in their upper incisors. A master cast was made for the upper incisor and was used to make a mass production mold to produce six casts per batch. The groove of the master cast was then filled with putty, and then molded again to produce cast teeth that lacked a groove and possessed a smooth labial surface. The resulting casts were identical in shape and size to the natural casts except for the absence of the groove. This was done in order to compare the forces required to break identically sized "incisors" of homogeneous composition and, therefore, test the hypothesis that the strength of the tooth is intrinsic to shape rather than enamel thickness or microstructure. This grooveless cast was likewise used to make a mass production mold of six casts per batch.

Replica incisors for the compression experiments were cast in USG ® Hobby Plaster using the recommended mixing ratio (65 parts water:100 parts plaster). Three batches of plaster were poured into the mass production molds to make 24 casts of both grooved and grooveless teeth. These casts were ground down to a standard length within the range of 3.2–3.8 mm (Fig. 1A). To prepare the experiments, 2 casts from each population were randomly selected to dial in the weight required to preload the experimental compression rig. After running the experiments on the remaining 44 casts, the largest 2 measurements from each population were excluded to

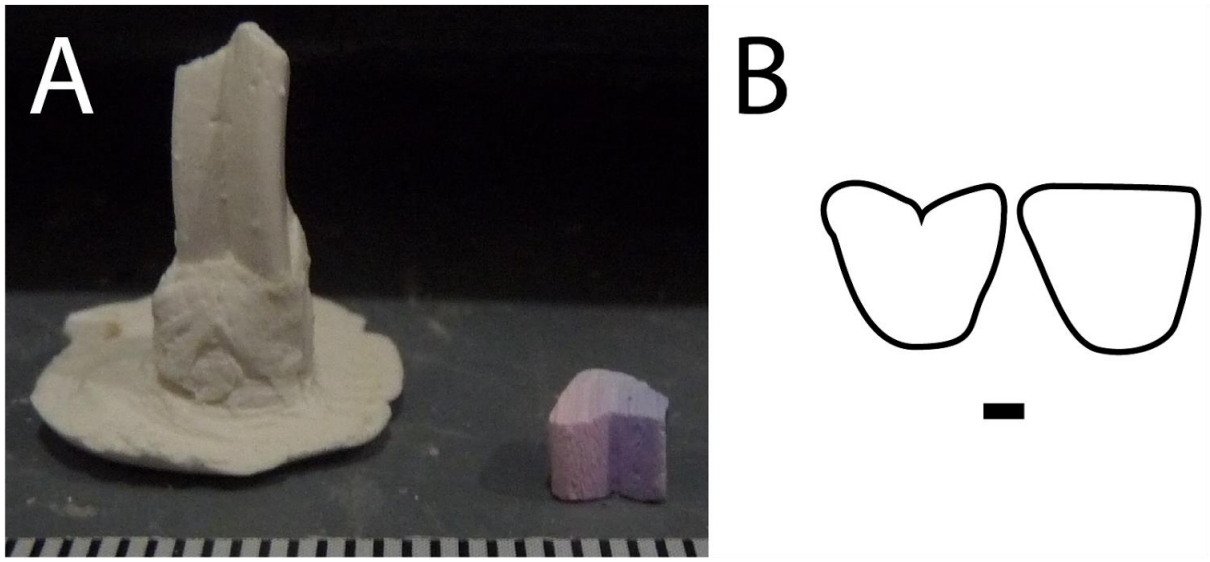

Figure 1—Comparison of groove and grooveless casts. A) Comparison of grooved cast before and after grinding. Color in cast on the left comes from separation of ink from labeling wet plaster. B) Comparison of the cross-sectional area of the casts. Scale bar 1 mm.

help account for human error, resulting in 20 measurements from each population and a total number of 40 experimental trials. The cross section of the casts was traced and measured in Image J (v1.48) and is shown in Figure 1B.

The experimental set up consisted of a ring stand sheathed in ⅞ inch (2.2225 cm) PVC pipe with an inverted ring stand dropped down into it (Fig. 2). The cast to be compressed was placed on the lower ring stand, then the ring stand was sheathed, and the inverted ring stand placed into the PVC pipe. After the upper ring stand was loaded, it was preloaded with 6.04639 kgs of weight (inclusive of the weight of 2 bricks and the inverted ring stand). A plastic bucket was placed on top and filled with water until the rig sank as a result of the compression failure of the cast. The weight of the bucket and water contained in it was noted, and this weight was added to the preloaded weight and recorded (Table 1). The weights required to generate failure were

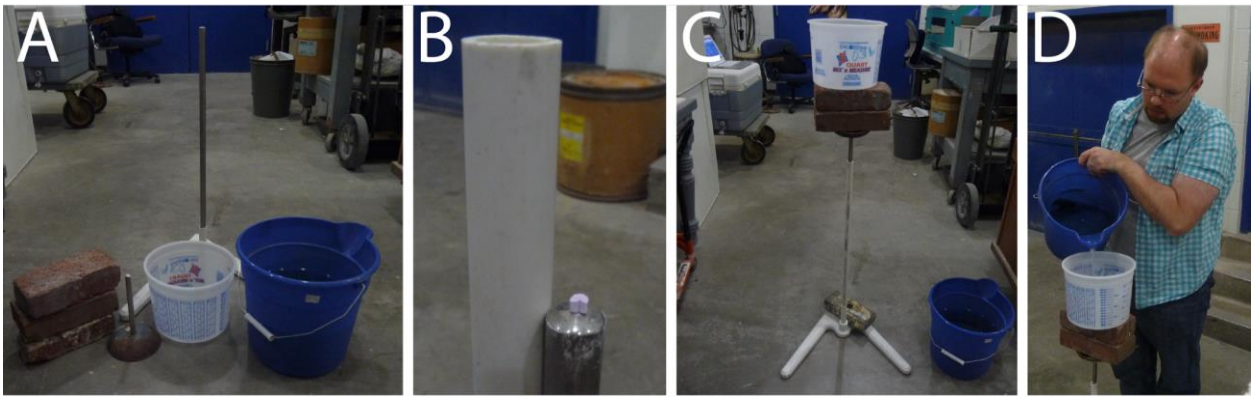

Figure 2—Experimental set up. A) Components of experimental setup: large ring stand, small ring stand (to be inverted and placed into PVC sheath), bricks for preloading weight, plastic bucket to receive added water, and water bucket (PVC sheath not shown); B) Placement of cast on lower ring stand and height of PVC sheath relative to the cast; C) Experimental set up prepared for trial; D) Addition of water to plastic bucket until cast failure—i.e., inverted ring stand crushes cast on larger ring stand in PVC sheath.

then compared using ANOVA in Microsoft Excel (Table 2). All the mass loaded onto the top of the cast was weighed on a digital scale in pounds and then converted to metric units.

To test the hypothesis that grooves in incisors correspond with diet, a literature review compiled data on the known diets of subterranean rodents, as well epigeal rodents and other glires that possess grooved incisors. The review of rodent behaviors and incisor morphology was grouped at the generic level, and the literature survey was combined with observations made on the wear patterns of the incisors of different burrowing rodents held in the mammal collections of the University of Kansas. Grooved incisors were documented in 61 genera of extant rodents; 53 epigeal and 8 subterranean. The taxa, groove pattern, burrowing behavior, diets, and references are available in Appendices II–V. This raw survey of diets was classified into single groups of dietary preference (i.e., fruit, grasses, geophytes, invertebrates, leaves and green plant

Weight at failure in grooved cast	Weight at failure in grooveless cast
6.04639	6.97171768
6.36844032	6.9762536
6.39565584	7.2030496
6.40472768	7.32098352
6.43647912	7.59767464
6.54987712	7.81086288
6.58616448	8.28713448
6.66781104	8.541146
6.68595472	8.66815176
6.7494576	8.79515752
6.76760128	8.93577104
6.89007112	8.94030696
6.95810992	9.0400972
7.12593896	9.0854564
7.14408264	9.23060584
7.35273496	9.62523088
7.37541456	9.84295504
7.52509992	9.8792424
7.5659232	10.44169648
7.80179104	10.6503488

Table 1—Weights required to generate cast failure in experimental trials.

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	20	137.3977255	6.869886276	0.224268176
Column 2	20	173.8438427	8.692192136	1.229501883

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	33.20798647	1	33.20798647	45.68533556	5.21859E-08	4.098171731
Within Groups	27.62163119	38	0.726885031			
Total	60.82961759	39				

Table 2—ANOVA table comparing the weight required for tooth failure in grooved versus grooveless casts.

matter, roots, or seeds) based on the primary feeding preference described. The summary of the relative frequency of diet types for epigeal rodents with grooved teeth, subterranean rodents with grooved teeth, versus subterranean rodents and prolific burrowing rodents (i.e., *Aplodontia* and *Cynomys*) with grooveless teeth (Table 3) was tested using chi-square analysis in Microsoft Excel to evaluate the null hypothesis that diet does not correlate with lifestyle or presence of a groove (i.e., relative frequency of the different groups within a single dietary preference are equal). The wear pattern of the incisors was investigated to determine if the groove was accompanied by a change in occlusion pattern that could be related to diet.

Institutional abbreviations—**KU**, Mammalogy Collection, University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, Kansas; **KUVP**, Vertebrate Paleontology Division, University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, Kansas.

Diet	Relative frequency among epigeal rodents with grooved incisors	Relative frequency among subterranean rodents with grooved incisors	Relative frequency among subterranean rodents without grooved incisors
Fruit	0.056603774	0	0
Geophytes	0.018867925	0.285714286	0.421052632
Grasses	0.169811321	0.714285714	0.210526316
Invertebrates	0.075471698	0	0
Leaves and Green Plant Matter	0.169811321	0	0.052631579
Roots	0.037735849	0	0.315789474
Seeds	0.339622642	0	0
Diet unknown	0.132075472	0	0
n	53	7	19

Table 3—Comparison of dietary preference in epigeal rodents with grooved incisors, subterranean rodents with grooved incisors, and subterranean rodents with grooveless incisors.

RESULTS

Bathyergus suillus has a single deeply pronounced longitudinal groove in its upper incisors (Fig. 3A). The groove is quite wide and V shaped, and removes approximately 7% of the cross-sectional area of the tooth assuming that the incisor would have a flattened face.

There was a significant difference in the weight tolerance of the grooved versus the grooveless casts (Table 2). The natural, grooved casts could not support as much weight as the grooveless casts. There was almost not overlap in the distribution of the weights required to compress the casts to the point of failure. On average, the grooved casts could only support 6.87 kg before failure, and the grooveless casts could support 8.70 kg before failure. The area of the incisor cross section was 12.742 mm^2 in the grooved casts and 13.594 mm^2 in the grooveless casts.

The casts tended to fracture vertically or subvertically. Recovered fragments of the grooved casts showed that the fracture propagated along the groove. The grooveless casts tended to fracture in more complex ways, but in cases where the cast fragments were recovered, they also tended to be fractured along the vertical midline of the cast.

Subterranean rodents overall have similar dietary preferences (geophtyes, roots, and grasses), and a primary difference between the grooved and grooveless genera are the relative proportions that prefer to eat grasses. The difference in the proportion of grazing preference between subterranean genera that have grooves versus those that are grooveless is significant (chi-squared paired test, $P < 0.001$). The overwhelming majority (71%) of subterranean rodent genera with grooved incisors prefer a diet of grasses ($n = 5$). Geophytes are the only other major dietary preference for subterranean rodents with grooved incisors, though some of these rodents

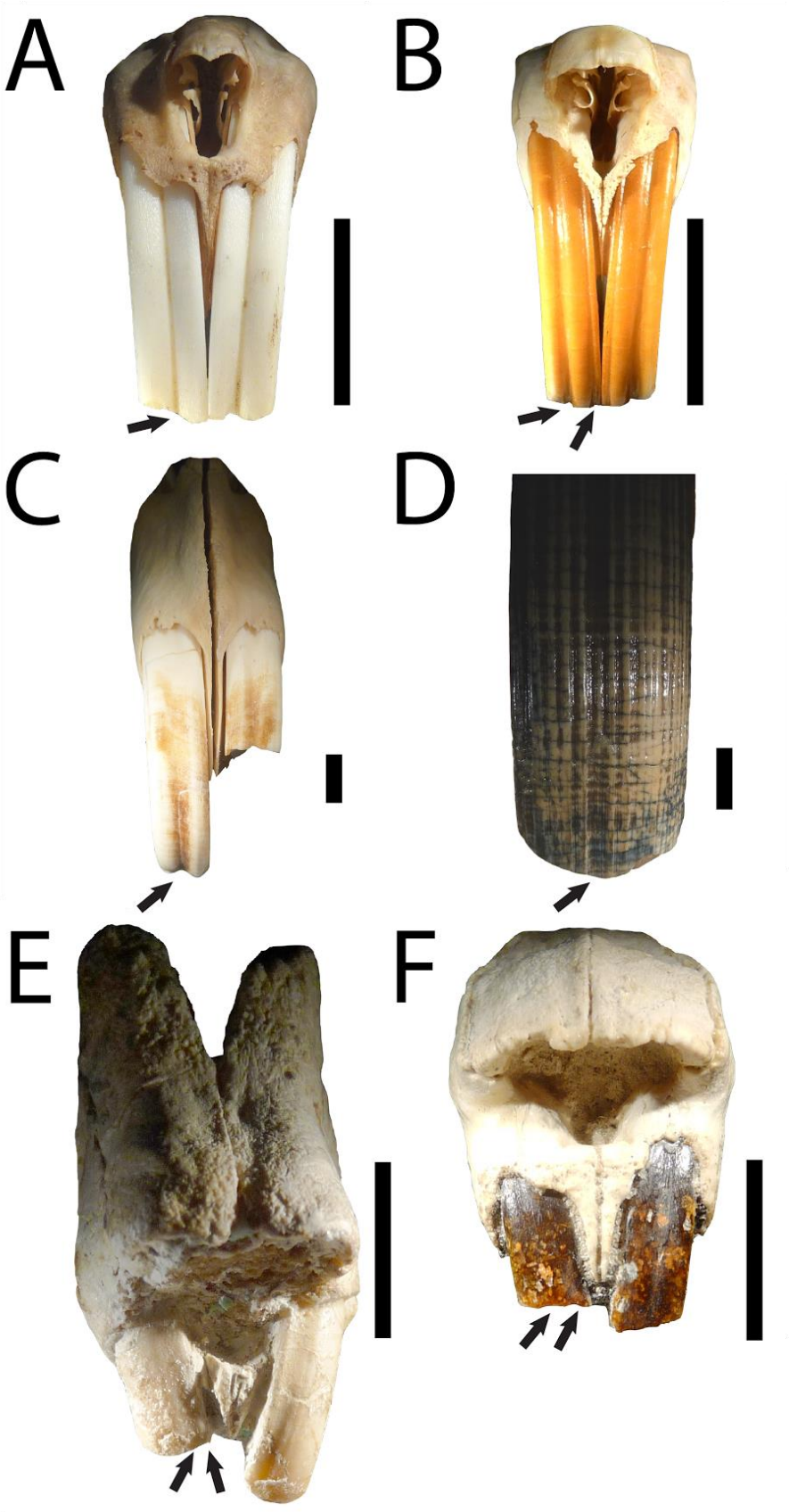
A
B
C
D
E
F

Figure 3—Upper incisors bearing longitudinal enamel grooves in representative rodent species. Arrows indicate position of grooves at the incisor tip. Scale bar height 1 cm. A) *Bathyergus suillus* (KU 1163992), a modern scratch-digging rodent with a single, medial groove on each incisor; B) *Geomys bursarius* (KU BAS 12), a modern scratch-digging rodent that with two longitudinal grooves on each incisor, one medially and the other closer to the sagittal plane of the skull; C) *Hydrochoerus hydrochaeris* (KU 158245), a modern semiaquatic browser with a single medial groove on each incisor; D) Distal portion of a single incisor of *Castoroides* sp. (KUVP 112771), a Pleistocene castorid interpreted as a semiaquatic browser with a large medial groove (indicated by arrow) and numerous small grooves across the enamel surface; E) *Ceratogaulus minor* (KUVP 6866), a late Miocene mylagaulid interpreted as a head-lift digger with several weak grooves near the sagittal plane of the skull; F) *Paraeuhapsis ellicottae* (KUVP 48015), an early Miocene palaeocastorine interpreted as a head-lift digger with two weak grooves on each incisor.

will take roots to supplement their diet. Rodents with grooveless incisors prefer roots or geophytes (i.e., bulbs, tubers, or corms) for a combined 74% of dietary preference for these genera. The major exceptions to this observation are *Ctenomys*, *Octodon*, and *Thomomys*, although *Thomomys* does eat forbs and roots as well.

As is to be expected from the relatively increased diversity and availability of food, epigeal taxa with grooved incisors consume a wider variety of foods by comparison to subterranean rodents, as epigeal rodents consume from all of the seven noted food categories. Seeds (~34%), grasses (~17%), and leaves and green plant matter (~17%), are the most commonly noted food items preferred by these species (Table 3). Seven of the epigeal rodents

with grooved incisors are poorly known, some only known from sparse skeletal remains (i.e., the groove-toothed flying squirrel, *Aeretes melanopertus*).

DISCUSSION

Much attention has been paid to the wear patterns of upper incisors in gliriform mammals, and there is intuitive support for the hypothesis that the incisor groove is used to control the wear pattern. The fact that numerous epigeal rodents possess this groove, such as *Otomys* (the groove-toothed rat, defined in part based on the presence of a set of longitudinal grooves on the upper and lower incisors), *Hydrochoerus hydrochaeris* (Fig. 3C), and the extinct *Castoroides* (Fig. 3D), seems to indicate that, at least for epigeal rodents, diet is the primary controlling factor for the presence of the groove. This has been demonstrated positively for *Castoroides*, which had unique groove patterns depending on the species. The 2 species of giant beaver, *C. leiseyorum* and *C. ohioensis*, specialized on different types of plants based on the unique wear facets of their incisors (C. Rinaldi, pers. comm., 2012). Lagomorphs also possess several labial grooves on the incisors, and tend to be grass specialists as well (Nowak 1999).

The geomyids *Cratogeomys*, *Geomys* (Fig. 3B), *Orthogeomys*, and *Pappogeomys*, the bathyergid *Bathyergus*, the arvicoline *Prometheomys*, and the spalacid *Nannospalax* are the only extant subterranean taxa whose incisors possess grooves. Each of these groups independently converged on the subterranean niche (Nevo 1999). *Geomys* and *Bathyergus* are scratch diggers who primarily rely on their enlarged claws to dig and use their teeth only to cut roots during burrowing behavior (Stein 2000).

Many rodents burrow only when the soil is wet from the rainy season (e.g., Jarvis and Sale 1971). The soil becomes sticky as a result of the increased moisture and may become

difficult to remove from the incisors if the rodent must cut roots or if it burrows with the teeth (i.e., chisel-tooth digging). A groove in the incisor enamel could potentially be useful to extract the teeth from sticky, moist soil. Though discrete empirical data to support this observation is lacking, the grooved casts were easier to remove from the silicon molds than the grooveless casts. This at least serves as anecdotal evidence to support the claim that this groove functions somewhat similar to a "blood groove", that is, the groove can help break the vacuum formed by pressing the teeth into the soil and eases the removal of the incisor from objects as suggested by Russell (1968). There is insufficient evidence in this study based on examining incisor morphology to comment further on the validity of this hypothesis, but it should be tested further.

Russell (1968) posited that a potential function of the grooves in the incisors of geomyids was to help extract the incisors from food items, and he compared the incisors functionally to the fuller of a bayonet. A fuller is a long, longitudinal furrow in a forged blade. The term "blood groove" has been applied colloquially to the fuller, because of the mistaken notion that the groove was added to blades to allow blood to flow out of a wound as a blade was pressed in and prevent the muscles of the victim from contracting and forming suction that would prevent the blade from being removed (Hollis 2010). The utility of the fuller for channeling blood has been challenged (e.g., Knoll 2012). The fuller instead was added to blades beginning in the Medieval period as a means to lighten and stiffen them (e.g., Davidson 1998; Denny 2006). This forging technique is the same conceptual basis for the I-beam, so comparisons of structural similarity between the grooves of rodent teeth and I-beams may be appropriate.

Grooved structures are found in nature as a means of strengthening a structure or increasing its surface area without increasing its overall volume. The keratin in the distal phalanx of mammals is corrugated (marked by numerous grooves and ridges), likely for this reason.

Some structures resemble an I-beam, including the mandible of many tetrapods (e.g., Weishampel 1993). An I-beam is capable of resisting compression forces that are applied parallel to the orientation of the web (i.e., strut portion of the beam), but torsional forces and forces perpendicular or oblique to the web render an I-beam ineffective (Chen and Atsuta 2008). A grooved incisor, which could be argued to resemble an I-beam, is mechanically most effective at resisting forces lateral to the incisor, rather than those directed labio–lingually or along the surface of the groove. A groove in an otherwise homogeneous cylinder (such as a grooved rodent incisor) would serve as a plane of weakness during compression; without inward folding and thickening of the enamel or other compensatory enamel microstructure, the grooved teeth of rodents are more likely to break under compression. This explains why the grooved casts failed under less weight than the grooveless casts in the compression experiments.

Rodents highly specialized in gnawing (e.g., tree squirrels) generally possess teeth that are narrow and deep rather than wide and shallow (as in *Geomys*). The specialized arrangement of their muscles as well as the morphology of their incisors enables them to deliver a specialized bite that can pierce durable but ultimately breakable objects (e.g., nuts, seeds); the jaws of all sciuromorphs are specialized for this function (Cox et al. 2012). The wide and shallow incisors of *Geomys* and *Bathyergus* have some limited use during soil excavation, but are primarily used to cut roots and to process food items. Some types of squirrels (e.g., *Rheithrosciurus*) have numerous grooves, as many as ten, in each incisor; the tooth in this case may not function as an I-beam but rather like an arcade structure, with each band of enamel between the grooves acting like a column in a structure designed to resist both compressional and torsional failure (Yeomans 2009). This explains why these rodents are capable of breaking very hard nuts (e.g., Krentzel 2014), despite one of the results of this study that grooves are regions modified to create

localized failure. This unique buttressing capability is certainly not a function of the incisor in *Bathyergus* or any other single- or double-grooved taxon, however.

No grooves were observed among the chisel-tooth-digging rodents examined in this study. *Heterocephalus glaber* (the naked mole rat) has been noted to possess a groove on its upper incisors (Stein 2000), but this was not seen in any of the individuals observed. Naked mole rats live in very hard clay and hardpan soils; these soils are in fact so hard that despite all of their adaptations for tooth digging, naked mole rats wait for seasonal rains to soften the soils so that they can dig (Jarvis and Sale 1971). Even if *Heterocephalus* does possess a groove, it is much fainter than the deep, pronounced groove of the only other bathyergoid bearing grooved incisors, *Bathyergus*, which secondarily reacquired scratch-digging behavior. Chisel-tooth-digging rodents, such as naked mole rats, have a greater percentage of enamel in their incisors relative to other burrowing rodents (e.g., van der Merwe and Botha 1998). This is a necessity to compensate for the enhanced wear rates their teeth endure. The incisors of chisel-tooth-digging rodents are furthermore compressed to increase the force exerted at the tip (Lessa 1990), as a way to increase the efficiency of burrowing. The fracture patterns observed in the casts after the compression experiments indicate that the stresses are directed along the midline of the tooth; the elevated forces endured by the teeth of chisel-tooth diggers, therefore, would make a grooved tooth highly disadvantageous and fracture-prone, and indicates that any burrowing rodent with grooved incisors could not have used a chisel-tooth digging strategy. The potential function of an incisor groove (if it exists) in a naked mole rat is unclear.

The strengthening hypothesis has little functional support. The majority of modern fossorial rodents bearing grooved incisors are scratch diggers that do not rely on their teeth for burrowing behavior. The only nonscratch digger, *Nannospalax leucodon*, is a head-lift digger

(i.e., it grapples the soil with its jaws while the powerful neck muscles twist the head to loosen soil; Hildebrand 1985). *Ceratogaulus minor* (a late Miocene mylagaulid) bears grooved incisors (Fig. 3E), but it has variously been interpreted as a head-lift digger (Fagan 1960) or a nonburrower (Hopkins 2005). Martin (1987) defined the clade of burrowing beavers (Palaeocastorinae) based on their flattened incisor enamel, but named the tribe Euhapsini for those beavers that were likely modified for head-lift-digging behavior, such as the Miocene *Paraeuhapsis ellicottae* (Fig. 3F), another fossil rodent with grooved incisors. Many modern scratch-digging rodents lack flattened enamel on the upper incisors, but they all have smooth surfaces. Such incisor parameters as enamel microsctructure (e.g., Martin 1997), amount of enamel (van der Merwe and Botha 1998), and degree of curvature (e.g., Merriam 1895; van der Merwe and Botha 1998) are likely to be of greater consequence in determining incisor strength than the presence of a groove. Any potential interpretation of chisel-tooth-digging behavior in these fossil rodents is unsupportable.

The presence of the groove has a strong correlation with a change in the wear pattern of the incisors. Incisors lacking a groove tend to wear into individual points, such that each incisor acts as an independent wedge. Incisors bearing grooves, on the other hand, display 2 notable changes in wear as a consequence of the groove. First, the incisors tend to wear more strongly on the lateral edge than the medial edge. This creates a slant to the cutting edge of the tooth where the medial side is longer than the lateral side, which effectively creates a single point when both incisors are together. Second, the edge of the incisor that bears the groove tends to wear more quickly than the surrounding enamel, creating a notch in the edge of the enamel wherever a groove occurs. In species with several grooves, this creates a serrated edge. The adaptive function of this wear pattern is to create a shredding edge that would be useful for clipping and

processing grasses, an explanation justified by the strong correlation of incisor grooves with grazing specialists.

Most subterranean rodents without grooves appear to prefer to consume geophytes. These underground plant storage organs are typically abundant, available despite seasonal variations in climate, and often toxic to other types of animals (Stein 2000). Some subterranean rodents prefer to harvest and store geophytes in their burrow systems in environments with low food availability (e.g., Nevo 1999). Geomyids tend to be selective about their diets, whereas some octodontids (i.e., *Spalacopus*) are more generalist feeders. The selectivity of diets in geomyids may create an evolutionary pressure for the groove to develop in geomyids, whereas the generalist nature of the other rodents permits them to retain the primitive grooveless condition.

CONCLUSIONS

The presence of a longitudinal groove in the upper incisors is shown to correlate most strongly with dietary preference than other factors. In subterranean rodents, there is a strong dietary preference among rodents with grooved teeth to eat grasses, whereas those with grooveless enamel prefer roots and geophytes. Among other epigeal rodents with grooved incisor enamel, there is some preference for eating grass, but seeds remain the preferred food item as is typical for most rodents. The occurrence of a groove in the enamel creates a notch or serration in the incisor tip that is most useful for shredding fibrous vegetation, and such rodents as *Bathyergus* and *Geomys* have likely evolved the groove in their incisor enamel as they diversified into the grazing niche. The groove has also been hypothesized to play a role in easing the removal of teeth from soil or food, but this hypothesis was not explicitly tested here and cannot be rejected without further study.

The incisor groove plays no role in strengthening the tooth as was previously hypothesized. Compression experiments with replica teeth show a clear strength difference between grooved and grooveless teeth, and the groove further serves as a point of weakness for the development of fractures under stress. The occurrence of a single or a few deep grooves in the incisor enamel likely would reduce the overall compressive strength of the tooth during powerful bites, therefore limiting dietary options and burrowing behaviors available to the rodents that possess grooved incisors. The occurrence of numerous grooves in the incisor enamel may serve the purpose of strengthening the tooth by creating a unique tooth architecture, this hypothesis should be tested further.

Fossil rodents found with a groove in their incisor enamel cannot be interpreted as chisel-tooth-digging rodents if they display other characters consistent with burrowing adaptations. The euhapsine beaver *Paraeuhapsis* and the mylagaulid *Ceratogaulus* for this reason should be regarded as head-lift diggers.

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INCISOR MORPHOLOGY AS AN INDICATOR OF BURROWING BEHAVIORS IN FOSSORIAL RODENTS

SUMMARY

The incisor morphology of extant burrowing rodents was evaluated to interpret behavior in fossil rodents. Fossorial rodents utilize one or more of the following behaviors to excavate their burrows: scratch digging using the manual claws; chisel-tooth digging using the incisors to scrape soil; and head-lift digging using the head and incisors in a twisting fashion to break soil free. The incisors of 91 modern and 24 fossil rodents were measured to collect the following parameters for burrowing rodents: length, width, eruption length (length from alveolus to incisor tip), wear-facet length, wear-facet angle, and procumbency angle. There is a significant correlation between burrowing behavior and wear-facet length:eruption length, wear-facet angle, and procumbency angle in the upper incisors. Thin, procumbent incisors with short, curved wear facets distinguish chisel-tooth diggers from wider incisors with elongated, flattened wear facets in head-lift diggers, with scratch diggers occupying an intermediate morphospace. These different morphologies finely discriminate between head-lift- and chisel-tooth-digging behaviors in the absence of any postcranial skeletal material. Palaeocastorine beavers evolved into the chisel-tooth-digging niche early in the late Oligocene, and some euhapsine beavers specialized in head-lift digging in the late Oligocene and early Miocene. Mylagaulids, including the horned taxon *Ceratogaulus minor*, adapted to head-lift digging later in the Miocene. Comparison of modern incisor morphology to extinct rodents permits a more refined interpretation of

behavior. These results agree for the most part with previously published reports but further refine interpretations of ancient burrowing behavior.

INTRODUCTION

Rodents are among the most prolific of living burrowing organisms, and numerous rodent lineages have adopted burrowing lifestyles (e.g., Nevo, 1999; Stein, 2000). Nearly every rodent is capable of digging behavior (Nowak, 1999), but the number of specialized, subterranean rodents is much less (Stein, 2000). Digging with the manual claws, referred to as scratch digging, is the most frequently used burrowing method (Hildebrand, 1985). Rodents use two additional tooth-digging behaviors involving the incisors: (1) chisel-tooth digging—the use of the incisors to scrape away soil—used by some pocket gophers (Geomyidae), degus (Octodontidae), tuco-tucos (Ctenomyidae), blesmols (Bathyergidae), naked mole rats (Heterocephalidae), and bamboo rats (Rhizomyidae); and (2) head-lift digging—anchoring of the incisors into the soil while the head is twisted to break the soil—used by blind mole rats of the family Spalacidae (Nevo, 1999). Much attention has been paid to the functional aspects of the different burrowing behaviors (e.g., Hildebrand, 1985), the morphological and physiological constraints on obligate burrowing rodents (e.g., Buffenstein, 2000; Stein, 2000; Samuels and Van Valkenburgh, 2009), and interpretation of rodent burrowing behaviors from both the ichnologic and body fossil records (e.g., Martin and Bennett, 1977; Gobetz, 2006; Martin and Gobetz, 2006).

Specialized rodent burrowers had their origin in the late Oligocene, though some authors have suggested that the origin of rodent burrowing began in either the late Eocene or early Oligocene (Sundell, 2003; Schmerge et al., in review). Two lineages of castorids independently evolved into the burrowing niche in the late Oligocene—the migmacastorines (i.e.,

Migmacastor), which are interpreted as chisel-tooth diggers based on the procumbency and length of the incisors (Korth and Rybczynksi, 2003), and the palaeocastorines (e.g., *Palaeocastor* and *Pseudopalaeocastor*), which used chisel-tooth digging to construct large spiral burrows pertaining to the ichnogenus *Daimonelix* (Martin and Bennett, 1977; Martin, 1987). Earlier examples of spiral burrows are known, but were likely constructed by multituberculates in the Eocene and Jurassic (Bown and Kraus, 1983; Raisanen and Hasiotis, 2012) and nonmammalian synapsids in the Triassic and Permian (Smith, 1987; Riese et al., 2011; Hasiotis and Fischer, 2014). The means by which these burrows were constructed is not as well understood as the behavior used to produce *Daimonelix*. Palaeocastorines diversified considerably in the late Oligocene through early Miocene (Martin, 1987), and a clade of castoroid beavers (Nothodipoidini) also evolved into chisel-tooth diggers in the early Miocene (Korth, 2007a, 2007b). Palaeocastorines became extinct by the end of the early Miocene, likely as a result of warming and wetting climate (Martin and Meehan, 2005). Beavers were replaced as the dominant burrowing rodent in North America by the mylagaulids in the mid Miocene (Martin and Naples, 2002). Mylagaulids have been interpreted as scratch diggers and head-lift diggers (Hopkins, 2005; Gobetz, 2006), so their rise is likely linked to the transition from "hard" (sensu Jarvis and Sale, 1971) soils to more sandy soils, which are more conducive to head-lift digging. The extinction of mylagaulids in the late Miocene opened the burrowing niche to geomyoids, which have since been the dominant group of burrowing mammals in North America (Martin and Meehan, 2005). Burrowing rodents clearly evolved multiple times (Martin and Naples, 2002), and even among beavers fossoriality evolved independently several times (Korth and Rybczynksi, 2003).

Burrowing behavior in ancient rodents has been interpreted in a variety of ways. *Daimonelix*, originally suspected to be a plant fossil or coral (Barbour, 1892; summarized in Schultz, 1942), was determined to be a rodent burrow when fossils of *Palaeocastor* were found in what was later determined to be the terminal chamber of the burrow (Peterson, 1905; Schultz, 1942; Martin and Bennett, 1977). Martin and Bennett (1977) evaluated numerous *Daimonelix* burrows from Nebraska and demonstrated that different size classes pertained to different species of *Palaeocastor*, and that the largest *Daimonelix* appeared analogous to the architecture created by modern prairie dogs (*Cynomys*). They also determined that *Palaeocastor* used a chisel-tooth digging strategy based on the presence of paired scratch marks on the burrow walls. Scratch-digging behavior for mylagaulids (Gobetz, 2006) and chisel-tooth digging behavior for geomyoids (Gobetz and Martin, 2006) has been interpreted based on the surficial morphology of their fossil burrows. Samuels and Van Valkenburgh (2009) compared the skull morphology of various palaeocastorine beavers with modern rodents using the range of observed burrowing behaviors. Comparative anatomy of rodent skeletons demonstrates that a forward-tilted occiput, broadened scapulae, enlarged olecranon processes, and enlarged claws are related to head-lift digging, whereas chisel-tooth diggers are characterized primarily by highly procumbent incisors (Hildebrand, 1985; Nevo, 1999; Stein, 2000).

While gross cranial and skeletal morphology can be useful in determining burrowing behavior in ancient rodents, this cranial morphology is not unequivocal for interpreting behavior. Some skeletal morphologies have numerous uses and correlates; for example, incisors external to the lips are common to most subterranean rodents, and enlarged claws are not unique to fossorial taxa. Presence of an organism or fossil in a burrow is not proof that it was the burrowmaker, as many organisms occupy and enlarge the burrows made by rodents (Nowak, 1999). Fossils not

attributable to *Palaeocastor* have been found in *Daimonelix* burrows, presumably either washed in, drawn there by *Palaeocastor* to gnaw on, or are evidence of predators entering the burrows (Martin and Bennett, 1977). Indeterminate surficial morphology on a burrow can leave room for interpretation of a potential tracemaker (i.e., Gobetz, 2006).

Upper incisor procumbency is the primary architectural difference between chisel-tooth-digging rodent incisors (strongly procumbent) and those of head-lift-digging rodents and scratch-digging rodents (i.e., recurved) that has been recognized (Hildebrand, 1985; Nevo, 1999; Samuels and Van Valkenburgh, 2009), but little attention has been paid to other characters of the incisors of fossorial rodents. Rodents are unique from other mammals by possession of their single pair of ever-growing incisors in the upper and lower jaws (Feldhammer et al., 2007), but rodent incisors likely have a variety of morphologies that affect their wear, strength, and function. Teeth are one of the primary means to interpret diet and jaw mechanics in mammals (e.g., Kay, 1975), so the use of incisors to interpret other behaviors involving the jaws seems reasonable. Numerous correlates have been found between the incisors of extant burrowing rodents and their particular burrowing behavior. High incisor procumbency correlates with chisel-tooth digging behavior (Agrawal, 1967; Lessa and Thaeler, 1989; Lessa, 1990; van der Merwe and Botha, 1998; Samuels and Van Valkenburgh, 2009). Van der Merwe and Botha (1998) also reported that the ratio of enamel:dentine in the incisors was greater in chisel-tooth digging bathyergids compared to scratch-digging bathyergids. Other more basic aspects of incisor morphology, such as incisor size and shape of the wear facet of the incisor, have not been evaluated to determine a correlation with burrowing behavior. Incisor morphology of extant subterranean rodents is herein investigated with the intent to determine correlations with different burrowing behaviors in modern rodents and interpreting burrowing behaviors in various

groups of extinct rodents. Well-preserved rodent fossils, such as the ones from the lower Miocene Harrison Formation of Nebraska, pose an opportunity to further refine the interpretation of burrowing behavior in some enigmatic palaeocastorines. The goal of this study is to associate incisor morphology with burrowing behavior in a variety of modern rodents, and then interpret burrowing behavior from incisor morphology in fossil rodents, with special attention paid to the beavers of the tribe Euhapsini.

Institutional Abbreviations—**AMNH** and **F:AM**, American Museum of Natural History, New York; **CM**, Carnegie Museum, Philadelphia; **KU**, University of Kansas Natural History Museum and Biodiversity Institute, Mammalogy Division, Lawrence; **KUVP**, University of Kansas Natural History Museum and Biodiversity Institute, Vertebrate Paleontology, Lawrence.

METHODOLOGY

Modern and ancient rodents were measured for this study. Ninety-one modern rodents housed in the University of Kansas Recent mammal collections were measured. Only rodents that were either regarded as prolific burrowers (e.g., *Cynomys*, *Marmota*) or subterranean (e.g., *Spalax*, *Heterocephalus*) were measured. The sampled taxa, their family designation, burrowing style, and collected measurements are included in Appendices VI–XII. Twenty-four extinct fossorial rodents from the subfamily Palaeocastorinae and family Mylagaulidae were measured for the purpose of interpreting burrowing behavior in fossil rodents of North America. Statistically significant measurements and interpreted burrowing behaviors for the fossil taxa are reported in Table 1.

Taxon	Specimen number	Upper Procumbency	Upper facet angle	Facet Length: Eruption Length	Predicted Habit
Palaeocastor cf. *nebrascensis*	F;AM 64221	102	154	0.821112006	Scatch
Palaeocastor cf. *nebrascensis*	F:AM 64225	105	154	0.840288925	Scatch
Palaeocastor sp.	CM 14231	123	132	1.472440945**	Chisel-tooth
Palaeocastor sp.	KUVP 155839	117	138	0.80740038	Chisel-tooth
Palaeocastor fossor	KUVP 28372	110	132	0.789613848	Chisel-tooth
Palaeocastor fossor	KUVP 28383	111	158	0.738414006	Chisel-tooth
Palaeocastor fossor	KUVP 28385	130	141	0.594040968	Chisel-tooth
Palaeocastor fossor	KUVP 48019	122	127	0.709409594	Chisel-tooth
Palaeocastor (*Capatanka*) *gaulodon*	AMNH 12897	138	141	0.988700565	Chisel-tooth
Palaeocastor (*Capatanka*) *magnus*	KUVP 28380	114	155	0.974229409	Chisel-tooth
Palaeocastor (*Capatanka*) *magnus*	KUVP 28386	126	152	1.353166987**	Chisel-tooth
Palaeocastor (*Capatanka*) *magnus*	KUVP 28388	83	153	0.525336091	Chisel-tooth
Palaeocastor penninsulatus	AMNH 6998	119	149	0.737849779	Chisel-tooth
Pseudopalaeocastor barbouri	KUVP 48018	102	142	0.884670487	Chisel-tooth
Unnamed new euhapsine	KUVP 125061	117	139	0.865598027	Chisel-tooth
Fossorcastor greeni	KUVP 80845	116	150	0.93516561	Chisel-tooth
Euhapsis martini	AMNH 10818	-	-	1*	Head-lift
Euhapsis platyceps	CM 1220	110	164	1.085840059	Head-lift
Euhapsis luskensis	F:AM 64589	115	163	1.00	Head-lift
Paraeuhapsis breugerorum	KUVP 28376	121	150	1.161358811	Head-lift
Paraeuhapsis ellicottae	KUVP 48015	-	-	1*	Head-lift
Ceratogaulus sp.	KUVP 5908	-	178	0.446531792**	Head-lift
Ceratogaulus minor	KUVP 6886	114	173	1.863945578	Head-lift
Mylagaulus laevis	KUVP 9808	-	-	1*	Head-lift

Table 1—Upper incisor measurements of fossil subterranean rodents. Measurements described in methods. Measurement followed with (*) denotes a case where the tip of the incisor was missing, but the wear facet was visible at the base of the alveolus and therefore would indicate a wear facet length:eruption length ratio of 1 or more. Measurement with (**) denotes a case where the incisor was likely not in life position.

Aspects of the incisor morphology of these rodents were compared for the purpose of determining what parameters of incisor morphology correlate with burrowing behavior. The measured incisor parameters are shown in Figure 1. Measurement of incisor width, length, and breadth was measured at the tip of the medial wall of the alveolus using digital calipers with an accuracy of 0.01 mm. Width, length, and breadth were measured for both left and right incisors when preserved, and were then averaged into a single measurement for graphing. The presence or absence of enamel grooves and the wear pattern at the tip of the enamel were noted. Measurement of the angle of incisor eruption was measured in accordance with the methodology of van der Merwe and Botha (1998). The positions of the measured angles are indicated in Figure 1B & C. Angle measurements for degree of procumbency and wear-facet angle were made using digital photographs and measuring angles to the nearest degree using-ImageJ (1.48v) software. Tests for significant correlations were performed using Microsoft Excel.

RESULTS

There was statistically significant difference in the width:length ratio of the upper incisors between the rodents of different burrowing styles (ANOVA, $p = 0.01622$). There is a significant difference between chisel-tooth diggers and scratch diggers (ANOVA, $p = 6.798*10^{-3}$) but no significant difference between head-lift diggers and chisel-tooth differs (ANOVA, $p = 0.09249$), indicating a correlation between increased incisor width and use of teeth to brace the skull during burrowing. Among the observed fossil rodents, the length:width ratios, as well as the incisor breadth, tended to be much greater than the majority of the extant rodents measured. The greatest observed length:width ratios occurred in the mylagaulid and euhapsine rodents. The upper incisors in some head-lift diggers are spaced so widely apart that they did not contact one

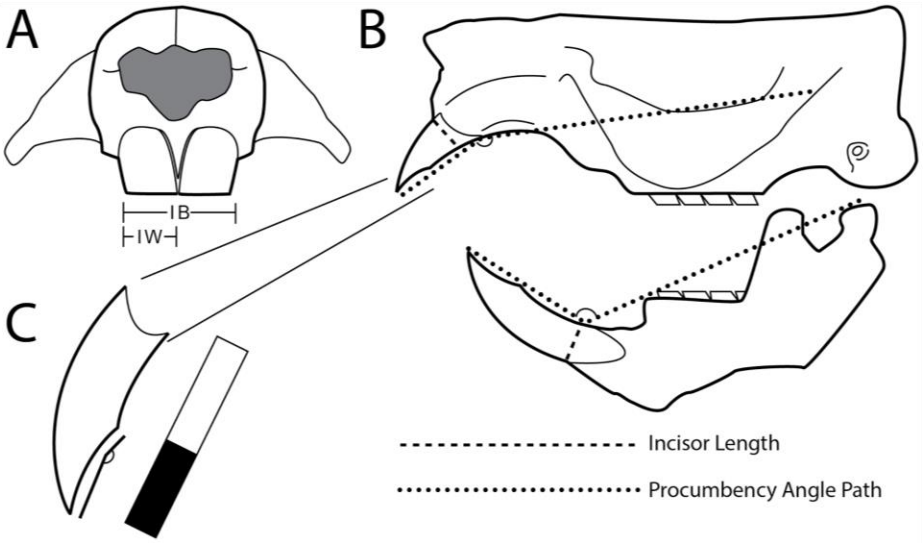

Figure 1—Schematic of measurements collected from the upper and lower incisors of the rodents in this study. A) Frontal view of skull showing incisor width measurements. B) Lateral view of the skull showing measurement of procumbency angles and incisor length. C) Closeup of tooth showing measurement of facet angle and wear facet characters. Length of black box indicates the length of the wear facet, and the combined length of the black and white boxes indicates the eruption length of the incisor. IB = incisor breadth, IW = incisor width.

another. There was no significant difference in the width:length ratio of the lower incisors (ANOVA, $p = 0.6936$).

The angle of incisor procumbency for the rodents measured is displayed in Figure 2. The most highly procumbent upper incisors occurred in chisel-tooth diggers. The incisors of extant head-lift diggers are external to the oral cavity and lips, and are therefore also somewhat procumbent but less so than in chisel-tooth diggers. The incisors of scratch diggers are nonprocumbent and are frequently recurved. There is a strong correlation between upper incisor procumbency and burrowing behavior (ANOVA, $p < 0.001$). The head-lift diggers constitute an entirely unique morphospace based on upper wear facet morphology, and there is significant

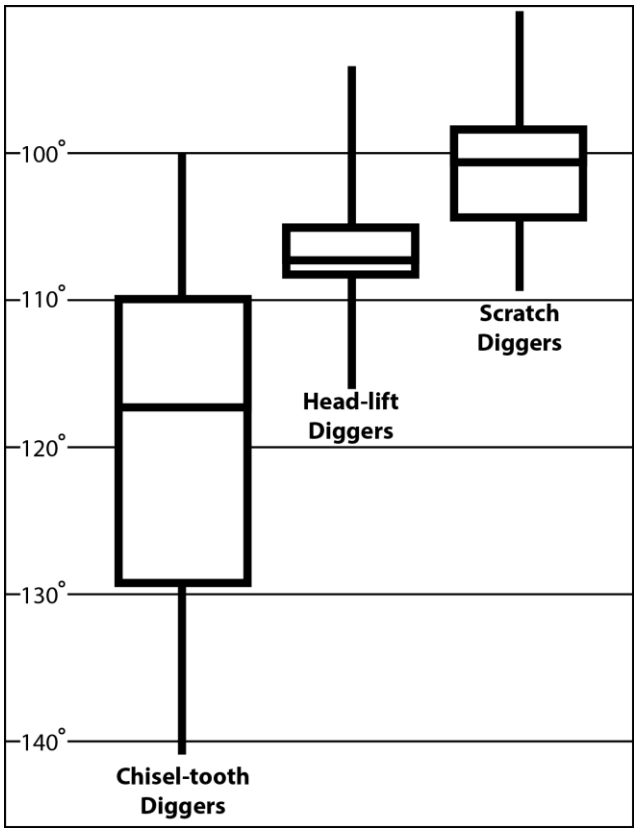

Figure 2—Box and whisker plots showing differences in upper incisor procumbency for modern rodents utilizing different burrowing strategies.

difference between chisel-tooth diggers and scratch diggers despite the slight overlap in their morphospaces (ANOVA, $p < 0.001$). There is no statistical correlation between lower incisor procumbency and burrowing (ANOVA, $p = 0.5865$).

A primary morphological difference between the incisors of extant rodents utilizing differing burrowing styles is the character of the upper wear facet. The angle of the wear facet is plotted against the relative length of the wear facet (facet length:eruption length) in Figure 3. Most chisel-tooth diggers exhibit shortened wear facets which appear highly curved when viewed in profile (Fig. 4). Modern bamboo rats (*Cannonomys* and *Rhizomys*; Fig. 4A) possessed some of the shortest wear facets, and in *Rhizomys* the wear facets are spatulate. Head-lift diggers

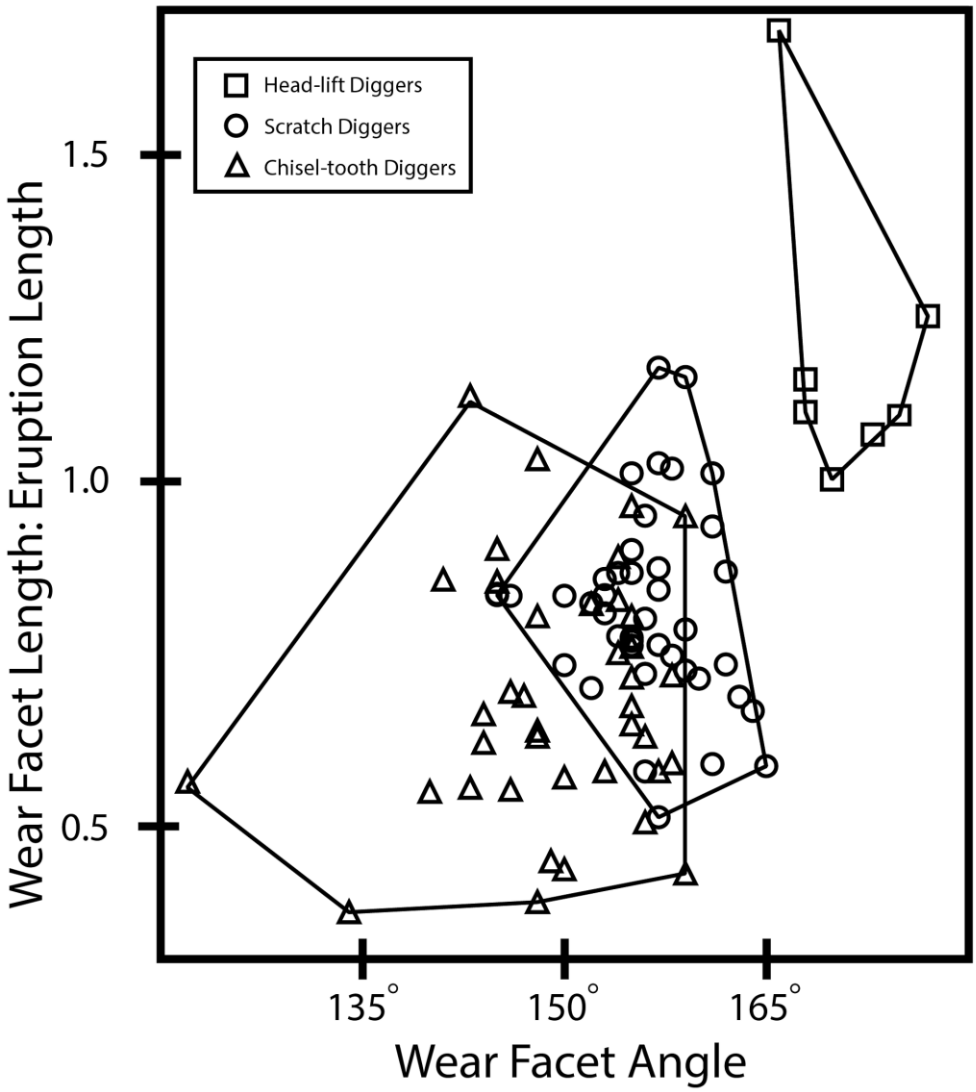

Figure 3—Plot of wear facet angle and wear facet length:eruption length. Morphospace separating groups is indicated.

contrast with this considerably and are characterized by possessing an elongated and flattened wear facet. In some specimens of *Spalax*, the wear facet is completely flat, and the only way to discern the edge of the wear facet in profile is to determine where the incisor length diminishes. The wear facet of head-lift digging rodents is elongate and approaches the alveolus in many

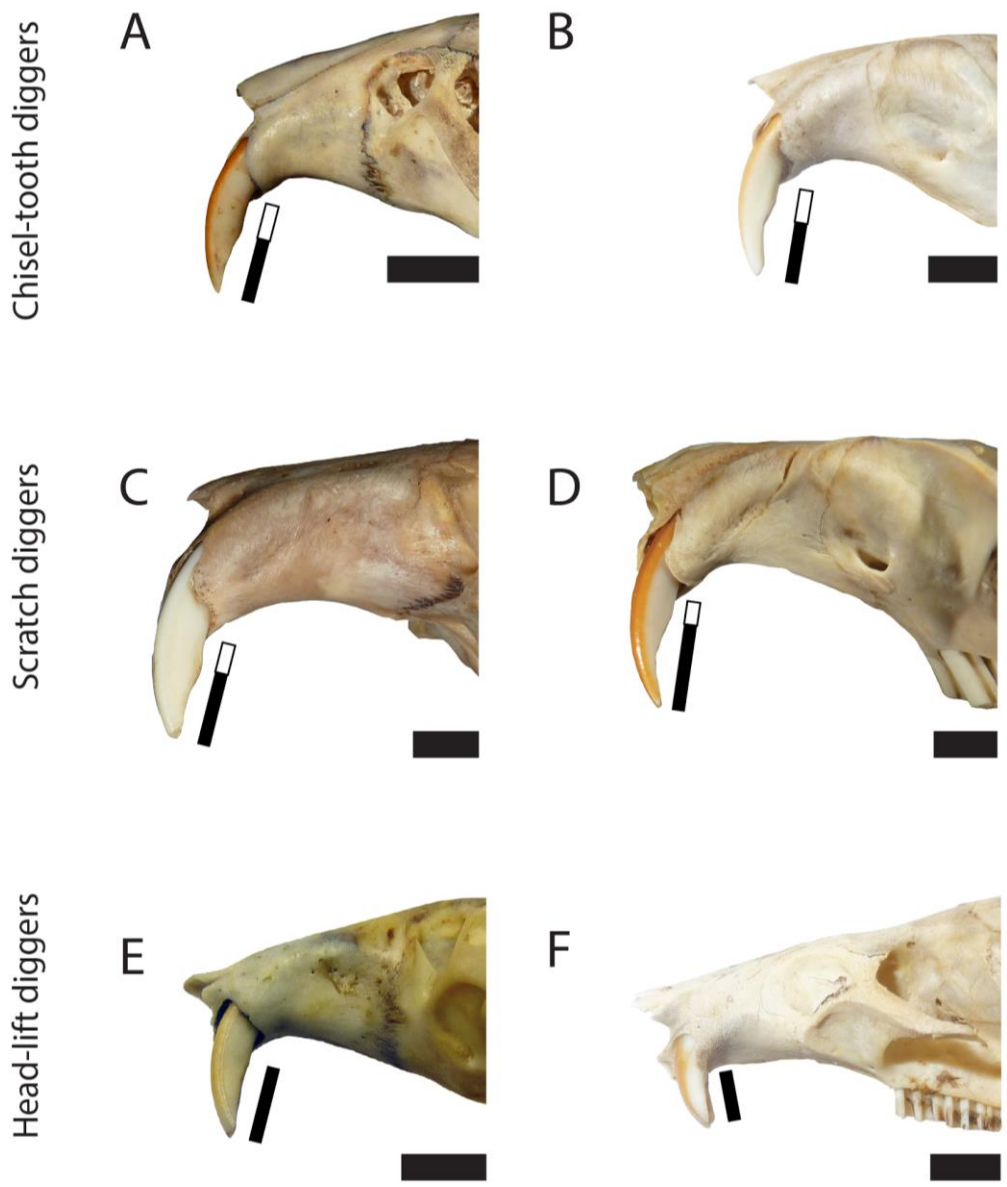

Figure 4—Lateral view of the upper incisor wear facets of modern subterranean rodents. Chisel-tooth diggers indicated by relatively short wear facets as in: A) *Tachyoryctes splendens* (KU 41126), B) *Thomomys bottae* (KU 23225; image reversed). Scratch diggers have moderate-sized wear facets as in: C) *Bathyergus suillus* (KU 163992), D) *Geomys bursarius* (KU BAS 12). Head-lift diggers have wear facets that form along most of the eruptive length of the incisor as in: E) *Nannospalax* (*Spalax*) *leucodon* (KU 102078; image reversed), F) *Myospalax baileyi* (KU 139554; reversed). Bars indicating length of wear and eruption as in Figure 1. Scale bar 5 mm.

cases. The wear facets of scratch diggers are moderately sized and curved, which are easily differentiated from the wear facets of head-lift diggers.

The extant rodents sampled in this study dominantly possessed a rounded or pointed wear edge on the incisors. In some cases, the edge of the enamel of the lower incisors wore into a concave margin on the edge of each upper incisor. Many bathyergoids possessed an edge that angled upwards toward the midline; this resulted in a single point when both incisors were aligned together. Rodents that bore a groove on the enamel surface developed either a notch or a series of serrations on the edge of the enamel in-line with the groove.

DISCUSSION

Procumbency

The relationship between burrowing behavior and incisor procumbency has been well documented by previous workers (e.g., Agrawal, 1967; Lessa, 1990; van der Merwe and Botha, 1998; Samuels and Van Valkenburgh, 2009), and results presented herein corroborate those studies. In bathyergid rodents, van der Merwe and Botha (1998) found a correlation between procumbent upper incisors and chisel-tooth digging behavior. Samuels and Van Valkenburgh (2009) sampled a wide variety of modern burrowers, and found that upper incisor procumbency was one of two variates that explained the majority of the morphological disparity among burrowing rodents. Van der Merwe and Botha (1998) found no relationship between lower incisor procumbency and digging behavior, but only considered 4 species from the family Bathyergidae. Samuels and Van Valkenburgh (2009) considered only the upper skull in their study. The question of whether both upper and lower incisors correlate with burrowing behavior among all subterranean rodents remained unanswered until now, and while upper incisor

procumbency relates strongly to burrowing behavior, there is no correlation between lower incisor procumbency and burrowing.

There are several reasons for the adaptive value of upper incisor procumbency. Procumbency serves to isolate the oral cavity—in conjunction with the closure of the lips behind the incisors—during excavation activity so that no soil is ingested (Stein, 2000). Chisel-tooth digging is accomplished by anchoring the upper skull in the soil while the lower incisors scrape soil from the burrow walls. Increased procumbency further enhances the ability to anchor the upper skull to the roof of the burrow during excavation, and is related to the adaptive requirements of increasing the growth rate of the tooth (Lessa, 1990). Increased enamel is laid down by the lengthening of the socket and addition of ameloblasts; the length of the incisor, therefore, can only be increased by either maintaining the same curvature and increasing the elevation of the rostrum or by increasing the path of the arc of the incisor, therefore, pushing the base of the root caudally and increasing procumbency. For these reasons, the incisors of all chisel-tooth-digging rodents and some head-lift-digging rodents are greatly elongated and visible when the lips are closed.

Incisor morphology

The wear facet has a genetic (i.e., evolutionary) component—the angle at which the incisor erupts—but also behavioral and environmental components, which are the way the tooth is used during life and the material on which it is used. The morphology of the incisor wear facet is determined by a combination of three factors: incisor growth rate, wear rate, and method of jaw occlusion. Rodents with high wear rates relative to growth rates produce shorter wear facets due to the considerable use of the teeth. Chisel-tooth digging rodents do have high absolute

growth rates (e.g., Howard and Smith, 1952; Miller, 1958; Rinaldi and Cole, 2000), but the wear rate on their teeth is so high that they do not need to gnaw on objects other than the soil and geophytes (e.g., rock, bone; Gobetz and Hattin, 2002) to keep pace with the growth rate of their incisors (Stein, 2000). Rodents with relatively low wear rates have long wear facets. Head-lift digging rodents use their incisors to cut roots and process food, but their incisors do not scrape soil during burrowing as in chisel-tooth digging. The upper inciosrs instead are used to anchor the skull to the soil while the powerful neck muscles break the soil loose (e.g., Hildebrand, 1985; Wake, 1993; Nevo, 1999). Head-lift digging rodents, therefore, have relatively low wear rates on their teeth, and their teeth tend to grow very long relative to skull size when compared to other fossorial rodents. Rodents that produce greater anteroposterior jaw motion also produce relatively shorter wear facets. Chisel-digging and scratch-digging rodents, therefore, tend to have shorter and more highly curved wear facets, whereas head-lift digging rodents tend to have longer wear facets.

The upper incisors appear to be more consistently diagnostic by comparison to the lower incisors (Fig. 3). All head-lift diggers are characterized by a ratio of the wear facet length:eruptive length in the upper incisors > 1, likely a consequence of the low growth rate of the incisors. Among chisel-tooth diggers, a ratio > 1 was only observed twice, and only six times in scratch diggers. This never occurred consistently in the same taxon of chisel-tooth or scratch digger, so any number of factors could possibly produce this artifact in these individuals including: advanced wear or lower incisor growth rates due to old age, increased soil or geophyte hardness, or unnatural wear resulting from the capture or captivity of the specimen. Head-lift diggers consistently have the most elongate wear facets. In chisel-tooth-digging rodents, the wear facet is typically < 60% of the length of the incisor eruption. The shape of the wear facet appears

to be a useful character for diagnosing burrowing behavior regardless of whether it occurs in the upper or lower incisors. The wear facet is consistently elongate and flat in head-lift-digging rodents, whereas it is curved in scratch- and chisel-tooth-digging rodents. The shortness of the wear facet highly exaggerates the curvature in chisel-tooth diggers, so they are distinct from scratch diggers (Fig. 3).

Grooves are present in the upper incisors of several rodents. This groove has the effect of creating a notch or a serration pattern along the tip of the incisor as it wears down. The cutting edge of all rodent incisors endures high wear, and tooth-digging rodents experience particularly high wear; Bennett and Faulkes (2000) reported that bathyergids lose shards of their teeth as they cut soil. The mechanical advantage of a cutting notch for burrowing behavior is dubious; though chisel-tooth diggers do use their incisors to cut roots—they do not require a specialized morphology to do so. Further, there is no mechanical advantage attributable to a notched incisor for digging in soil. Just as a pickaxe utilizes a single sharpened point to pierce soil, the incisors of chisel-digging rodents benefit maximally from a single point rather than two or more cutting edges. The serrated cutting edge interpreted for *Castoroides* would provide no benefit to burrowing in a chisel-tooth-digging rodent. For a serrated edge to cut, the plane of the serrations must move perpendicularly into the surface. The teeth of chisel-tooth diggers function optimally as scrapers (van der Merwe and Botha, 1998).

Grooves were observed among both scratch diggers and head-lift diggers, but never in chisel-tooth diggers. The deepest groove was seen in the bathyergid *Bathyergus*, the only scratch digger among the bathyergids. *Thomomys*, which lacks a groove, is the only extant geomyid rodent to prefer chisel-tooth-digging behavior; all other extant geomyids have one or more grooves in their enamel and prefer scratch digging, though some have the capacity for chisel-

tooth digging (i.e., Lessa and Thaeler, 1989). Chisel-tooth digging rodents would likely neither benefit from nor be capable of preserving a cutting notch akin to the one present in *Bathyergus* or geomyids such as *Geomys* or *Cratogeomys*. Only the naked mole rat (*Heterocephalus glaber*) has been reported among the modern chisel-tooth-digging rodents to possess such a groove (Stein, 2000), but the groove was only perceivable when seen under a microscope and was not seen in all individuals. The groove of *Paraeuhapsis*, though weak by comparison to *Bathyergus*, is much stronger than the groove of *Heterocephalus*. A groove was present in the upper incisors of two of the three investigated *Nannospalax leucodon* (a head-lift digger), and this groove appears similar to that seen in the fossil taxa *Paraeuhapsis* and *Ceratogaulus*. The functional implications of this groove should be investigated, but clearly a macroscopically observable groove never occurs in a primarily chisel-tooth-digging taxon. *Paraeuhapsis* was likely a head-lift digger based on this character (Fig. 5), as well as the other characters of its skull (Martin, 1987). While the presence of a labial groove in the incisor enamel is not sufficient alone to diagnose head-lift-digging or scratch-digging behavior, the occurrence of a pronounced groove in the enamel surface can rule out chisel-tooth digging as a behavior in fossil taxa because such a groove never occurs in association with chisel-tooth digging.

Rodents that use their teeth in burrowing behavior (i.e., chisel-tooth digging and head-lift digging) have comparatively wide incisors. The mechanical advantage of the relatively widened tooth cross section would disperse the bite force across the tooth against the applied anteroposterior direction of the bite force. The skull must be braced in the soil, so the incisors may be widened to resist any torsion forces created during jaw closure; this concern is especially true for head-lift digging rodents, which rely on twists of the head once the skull is engaged in the soil to dig their burrows.

Tooth-digging rodents are unique among mammals in that some possess a gap between the incisors of the lower jaw. Such head-lift-digging rodents as mylagaulids, spalacids, and *Paraeuhapsis* are further unique in that they possess gapped upper incisors as well. Increasing the gap between the upper incisors would likely serve an adaptive function for bracing the skull. Head-lift digging is not accomplished directly by the teeth; rather, both the upper and lower incisors grapple the soil while the powerful neck muscles twist the head until the soil gives way (Wake, 1993). The wear facets of head-lift taxa may be elongate, therefore, because it helps the teeth to grip the soil by penetrating deeply. Such chisel-tooth-digging taxa as modern naked mole rats (*Heterocephalus glaber*) and the fossil taxon *Palaeocastor*, by contrast, tend to have thinner teeth with shortened wear facets that rise to a point medially. This may certainly be an adaptation to digging in hard soils; chisel-digging geomyids live in more clay-rich soils than scratch-digging geomyids (Lessa and Thaeler, 1989), and naked mole rats live in extremely hard soils (Jarvis and Sale, 1971). Tooth-digging rodents have conservative upper incisors that are used only to brace the skull of the animal while the lower jaws scrape the soil (Lessa, 1990). The loose sediment is then pushed away by the limbs, either by the front limbs as does *Tachyoryctes* or the hind limbs as does *Heterocephalus* (e.g., Jarvis and Sale, 1971).

The lower incisor wear facet morphology may not correlate with burrowing behavior for a variety of reasons. Previous attempts to identify unique incisor morphology with burrowing behavior likewise failed to demonstrate a difference in the lower incisors between different burrowing styles (e.g., van der Merwe and Botha, 1998). The upper incisors in tooth-digging rodents are used for bracing the skull, but the lower incisors are responsible for handling and processing food in addition to burrowing (Agrawal, 1967). Variations in diet and food processing requirements among different burrowing rodents—and even among individuals of the same

species—create complex interactions in the ways tooth shape forms. Since the lower incisor scrapes the soil during chisel-tooth digging (Jarvis and Sale, 1971), the shape of the wear facet can be highly variable in chisel-tooth diggers depending on how dulled the tooth has become from bouts of burrowing activity. This also relates to factors that make the soil more resistant to tooth digging, such as increased clay content and formation of hardpan textures, so different chisel-tooth digging rodents may have lower incisor morphologies that correlate with the local soil conditions. Different rodent species primarily rely on one type of digging behavior, but may supplement this with another burrowing strategy, so the lower incisor morphology may appear more variable as a result.

Though no significant difference was found in lower incisor morphology, work should continue to determine how burrowing behavior shapes the morphology of the lower incisors beyond the scope of this study. Studies on the growth rates of the incisors indicate higher growth rates in the incisors of chisel-tooth diggers (Miller, 1958; Marano, 1959; Zuri et al., 1999) and much higher overall growth rates in fossorial rodents compared to nonfossorial glires (Hildebrand, 1985). These high growth rates may serve to overprint the difference in morphology, but a study of growth increments may reveal a morphology unique to chisel-tooth digging rodents. Despite the lack of difference in procumbency, which could have been a phylogenetic artifact, van der Merwe and Botha (1998) did report a nearly 10% difference in the enamel content of the incisors of chisel-tooth diggers compared to scratch diggers, and similar results have been reproduced in other chisel-tooth-digging rodents (e.g., Flynn et al., 1987; Buzas-Stephens and Dalquest, 1991; Justo et al. 1995). Future study of the enamel content of the lower incisors of burrowing rodents could reveal correlations for other rodent groups as well, and could be useful in interpreting burrowing in fossil taxa.

Interpretation of behavior in fossil rodents

The morphology of the wear facet can be applied to fossil rodents to interpret their behavior (Table 1), even for those fossils not found in burrows. The early palaeocastorine, *Palaeocastor* cf. *nebrascensis*, has nonprocumbent incisors and a somewhat elongated wear facet, confirming previous interpretations of scratch-digging behavior (Samuels and Van Valkenburgh, 2009). *Pseudopalaeocastor barbouri*, *Palaeocastor fossor*, and *Palaeocastor magnus*, known to be chisel-tooth diggers based on the surficial morphology of *Daimonelix* burrows (Martin and Bennett, 1977) and cranial structure (Samuels and Van Valkenburgh, 2009), are confirmed in this study to be chisel-tooth diggers based on the shortness and curvature of their wear facets (Fig. 5A–C). The primitive euhapsine beavers, such as *Fossorcastor*, also had procumbent incisors with shortened wear facets consistent with interpretation of chisel-tooth digging. The wear facets of the derived euhapsine beavers *Euhapsis platyceps* and *Paraeuhapsis breugerorum* (Fig. 5E–F) are instead worn from the tip of the incisor to the alveolar margin and the wear facet is flat rather than J-shaped, as seen in modern *Spalax*. This is strong evidence that these euhapsines were head-lift diggers and convergent with modern head-lift diggers on this morphology and behavior. Complete incisors are not known from *Paraeuhapis ellicottae*, but it can also be interpreted as a head-lift digger based on the presence of a groove in the enamel of its incisors and the occurrence of a flattened wear facet on the remaining portion that extends to the alveolus (i.e., wear facet length:eruption length ratio > 1).

Mylagaulids have been variously interpreted as head-lift diggers (e.g., Gidley, 1907; Fagan, 1960) based on the similarity of their cranial anatomy to living head-lift diggers and as surface-dwelling grazers (Hopkins, 2005). There is no published record of mylagaulids from

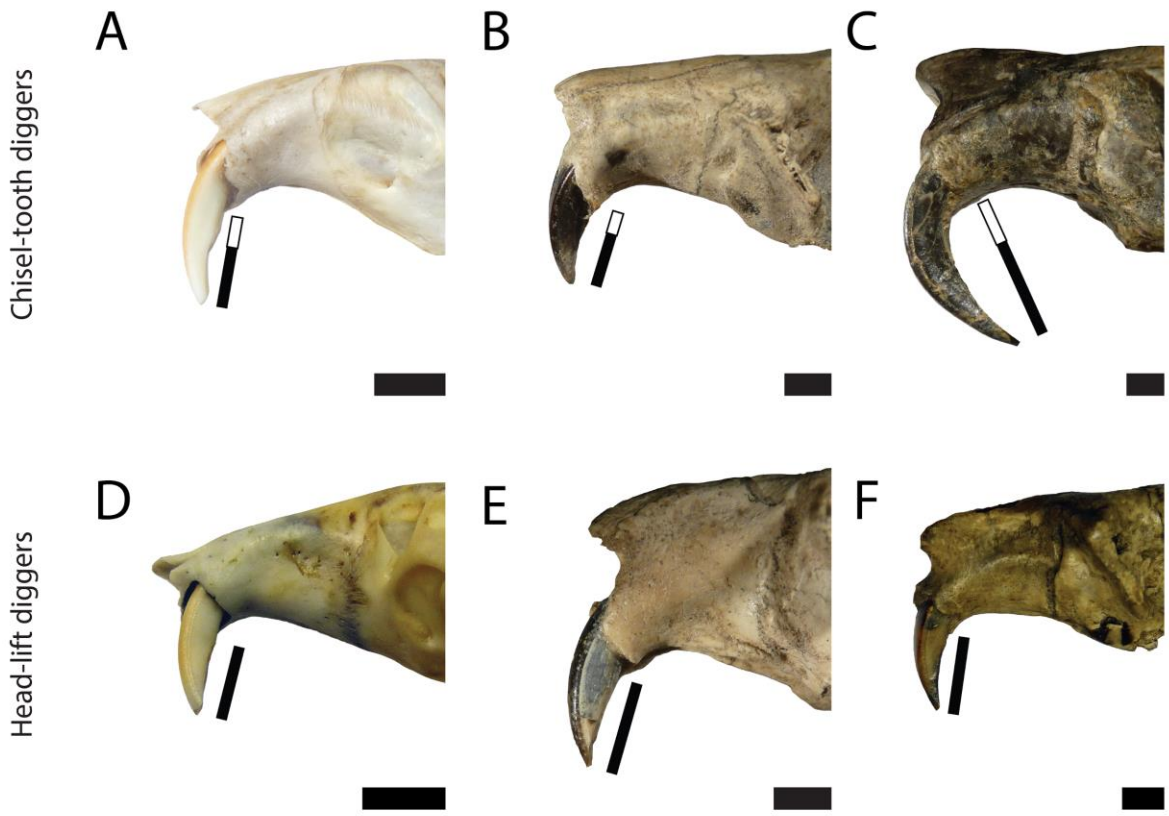

Figure 5—Lateral view of the upper incisor wear facets of modern rodents compared to extinct palaeocastorine beavers interpreted as subterranean burrowers. Relatively short and curved wear facets of A) modern *Thomomys bottae* (KU 23225; image reversed), suggests B) extinct *Palaeocastor fossor* (KUVP 28383) and C) extinct *Palaeocastor magnus* (KUVP 28388) are both chisel-tooth diggers. Elongate and flat wear facets of D) *Nannospalax* (*Spalax*) *leucodon* (KU 102078; image reversed) are highly reminiscent of those in E) extinct *Paraeuhapsis breugerorum* (KUVP 28376), and F) extinct *Euhapsis platyceps* (CM 1220) and indicate they are head-lift diggers.

burrows; however, many specimens have likely been collected from burrows (see detailed discussion in Gobetz, 2006). Only one ichnotaxon (*Alezichnos chelecharatos*) has been attributed

to mylagaulids, based on the similarity of the surficial morphology to experimental markings made with the claws of the stratigraphically contemporaneous mylagaulid *Pterogaulis laevis* (Gobetz, 2006). Gobetz (2006) described the tracemaking behavior as scratch digging, which is typically a secondary behavior associated with head-lift digging. The architecture of the ichnotaxon *Alezichnos* is consistent with the burrows of specialized, subterranean rodents; the robust manus of *P. laevis*, while adapted for some scratch digging, is clearly more robust than that of a surface forager (e.g., *Cynomys* or *Spermophilus*). *Myospalax* is a modern rodent that utilizes both scratch and head-lift digging (Nevo, 1999; Stein, 2000), and comparisons of their skulls and forelimbs to those of *P. laevis* are favorable. The tooth morphology of *P. laevis* described in this study is consistent with such an interpretation. The skull morphology of the closest living relative to mylagaulids, *Aplodontia rufa*, is reminiscent of the morphology of mylagaulids and other head-lift diggers, leading some to suggest that it could be a head-lift digger (Samuels and Van Valkenburgh, 2009; Druzinsky, 2010). The wear-facet morphology of *Aplodontia*, however, is clearly short and curved as one would expect from a scratch digger. The incisor morphology of *Aplodontia* is clearly different from *Ceratogaulus*, which has elongate and flat wear facets in the upper incisors (Fig. 6). This finding supports both the argument that *Aplodontia* is a scratch digger and that the horned *Ceratogaulus* was a head-lift digger.

Implications for convergent evolution of subterranean rodents

As organisms evolve in response to changing environmental and climatic conditions, they converge on body plans that are ideally adapted to specific combinations of environmental factors, a phenomenon referred to as ecomorphy (Williams, 1972). Ecomorphs converge so closely in morphology that confusing unrelated organisms as being closely related is possible,

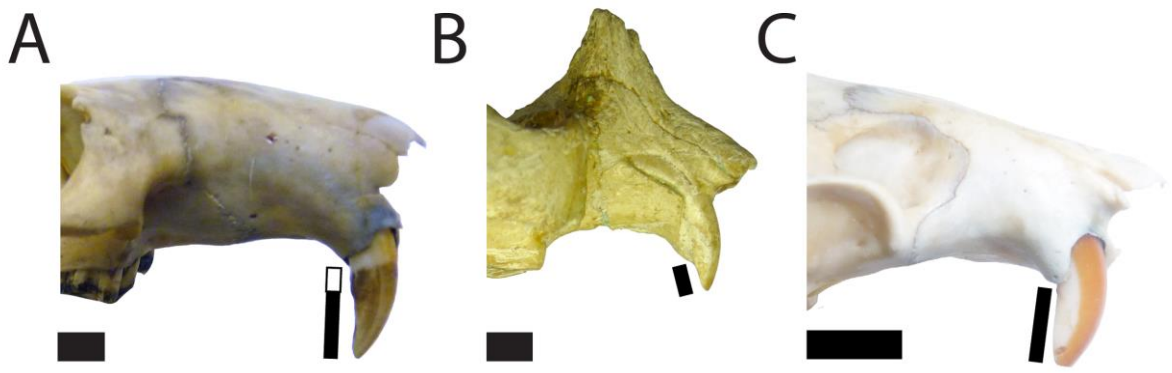

Figure 6—Comparison of the incisor wear patterns of the extant *Aplodontia rufa* (KU 143976) and the extinct *Ceratogaulus minor* (KUVP 6886). The wear pattern in *A. rufa* is consistent with scratch-digging behavior, whereas the wear in *C. minor* indicates head-lift digging behavior. The upper incisor morphology is more similar to the head-lift digging C) *Myospalax baileyi* (KU 139557) which also possesses an elongate and flat upper incisor wear facet, as a result of head-lift digging.

and similar faunas have evolved independently through time from widely unrelated groups (e.g., Martin and Meehan, 2005). The subterranean niche is stable and predictable (Nevo, 1979), so application of the ecomorph concept to burrowing rodents allows for interpretation of behavior and ecology of extinct rodents based on their skeletons.

Species assigned to *Palaeocastor* are commonly compared to modern prairie dogs (*Cynomys*). Some aspects of their behavior were likely very similar; they both constructed dwellings that lasted for many generations, and they were both gregarious (Martin and Bennett, 1977). *Palaeocastor* created storage larders in its burrows (i.e., *Daimonelix*), evidenced by the presence of dense aggregates of seeds and plant material in some chambers (Schultz, 1942). Martin and Bennett (1977) deduced from the depth of the burrows of *P. fossor*, which were too deep to access roots or geophytes from within the burrow system, that it must have been a

surface grazer similar to prairie dogs. *Palaeocastor*, however, excavated burrows using chisel-tooth-digging behavior, whereas prairie dogs are scratch diggers (Martin and Bennett, 1977). This is likely a function of soil hardness. Prairie dogs prefer sand- and clay-loam soils (e.g., Reading and Matchett, 1997). The paleosols preserved within the Harrison Formation were formed in silty to sandy overbank deposits (Yatkola, 1978). *Palaeocastor* was not similar to prairie dogs, but was instead most similar to the living tuco-tuco (*Ctenomys*), which excavates large, unplugged burrow systems with its incisors and emerges to the surface to forage (e.g., Giannoni et al., 1996). The burrow systems of modern rodents should still be thoroughly investigated to evaluate the uniqueness of the morphology of *Daimonelix*.

Euhapsine rodents show examples of both chisel-tooth and head-lift digging. Martin (1987) argued that the early members of the Euhapsini, the genus *Fossorcastor*, were convergent with bamboo rats (*Rhizomys*) based on their skull shape; that comparison is even further supported based on the shape of their incisor wear facets. The genera *Euhapsis* and *Paraeuhapsis* are both marked by elongate flat wear facets and are most consistent with the incisor morphology of head-lift diggers, which agrees with previous interpretations based on their skull morphology.

The mylagaulids sampled in this study clearly show incisor morphologies that are most similar to living head-lift diggers, and these morphologies are not similar to that of their closest living relative, *Aplodontia*, a scratch digger. There are burrows attributed to hornless mylagaulids, but no burrows of horned mylagaulids have yet been described. While some prefer the hypothesis that horns were a defense mechanism for these mylagaulids (i.e., Hopkins, 2005), their incisor morphology indicates they were burrowers. The behavior of these enigmatic rodents should continue to be investigated.

Interpretation of behavior from the skeletons of ancient animals is frequently the only means by which to interpret their lifestyle, such as the homeothermic habit of *Thrinaxodon* (e.g., Hillenius, 1994) and flight capability of pterosaurs (e.g., Chatterjee and Templin, 2004). Many species of burrowing beavers have been found inside of their burrows (e.g., Peterson, 1905; Schultz, 1942; Martin and Bennett, 1977), so interpretations of their behavior inferred from cranial anatomy can be verified based on the architectural and surficial morphology of their burrows (Martin and Bennett, 1977; Hasiotis and Mitchell, 1993; Hasiotis et al., 1993). The euhapsines are clearly adapted to burrowing behavior, based on their skull structure (Martin and Naples, 2002; Samuels and Van Valkenburgh, 2009), but they have not been found in burrows. Interpreting their burrowing behavior, therefore, requires interpretation based on the cranial and postcranial (when known) skeleton alone.

CONCLUSIONS

Upper incisor morphology corresponds well with burrowing behavior. Subterranean rodents using chisel-tooth-digging behaviors possess short, curved incisor wear facets. Scratch-digging rodents possess moderate-sized and somewhat curved incisor wear facets. Head-lift-digging rodents possess elongate and flat wear facets, which typically reach the alveolus in the upper incisors. These morphologies likely develop as a result of the interaction of incisor procumbency, growth rate, and wear rate. This morphology is clearly observable in the upper incisors, but the lower incisors have highly variable morphology that does not correspond with burrowing behavior. A macroscopically visible groove in the incisor enamel does not occur in chisel-tooth digging rodents, and its presence can help diagnose head-lift-digging or chisel-tooth-digging behaviors in combination with procumbency or wear facet measurements.

Many fossil groups can be interpreted as subterranean based on incisor morphology. Palaeocastorine beavers diversified into chisel-tooth-digging niches, as in the case of *Palaeocastor*, *Pseudopalaeocastor*, and *Fossorcastor*, and into the head-lift-digging niche in the case of the derived euhapsine beavers *Euhapsis* and *Paraeuhapsis*. All sampled mylagaulids appear to have been adapted to head-lift-digging behavior, but the mechanisms of their cranial morphology and burrowing strategies should continue to be investigated.

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CRANIAL OSTEOLOGY, ZYGOMASSETERIC SYSTEM, AND INTEGUMENTARY STRUCTURES OF THE MIOCENE BEAVER *PARAEUHAPSIS ELLICOTTAE* (RODENTIA: PALAEOCASTORINAE: EUHAPSINI)

SUMMARY

***Paraeuhapsis ellicottae* is a member of the Oligocene–Miocene palaeocastorine beaver radiation described as one of the best-adapted burrowing rodents of all time. Protrogomorphy, the attachment of the masseteric muscles to the zygomatic arches alone, is the primitive rodent condition but has been secondarily reacquired in this taxon. The unique cranial musculature of this rodent is herein reconstructed, and its function in burrowing is discussed. The presence of a unique keratinous structure attached to the nasal bones is suggested based on osteological evidence revealed using epi-illumination microscopy and micro-CT scanning. The nasal bones have a relatively increased degree of porosity compared to the surrounding maxillary bones, suggesting an increased presence of vascular and cartilaginous tissue associated with the nasals. The nasal rugosity is characterized by an annular zone of increased rugosity reminiscent of the dermal attachment sites for horns in rhinoceroses. Epi-illumination microscopy of the nasal bones of modern burrowing rodents reveals widespread Sharpey's fiber insertions for the purpose of anchoring a rhinarium, a keratinous pad covering the nasal region that resists abrasion and prevents soil from entering the nasal passages during burrowing activity. The surface of the nasal bones in *P. ellicottae* are marked by a number of sites of Sharpey's fiber insertions surrounding an enlarged nasal boss present at the symphysis between the**

two nasal bones, suggesting the attachment of a keratin fiber horn. The morphology and potential function of the horn in burrowing activity in *P. ellicottae* is discussed and compared with that of mylagaulids.

INTRODUCTION

Rodents are the most diverse order of mammals, comprising more than 2,000 recognized extant species, and new genera and families continue to be recognized. Rodents have diversified into nearly every niche occupied by mammals, including arboreal, gliding, semiaquatic, grazing, saltating, and burrowing forms (Nowak, 1999). Rodents possess some of the most specialized cranial muscles of any vertebrate group, as the masseter muscle is differentiated into several layers to facilitate the characteristic gnawing capability of rodents. Early rodents (e.g., *Paramys*) were characterized by masseter muscles with origins restricted to the zygoma, a condition referred to as protrogomorphy (Wood, 1965; Korth, 1994). In derived rodents, the origin of the masseter muscle extends onto the rostrum in one of three patterns: sciuromorphy, hystricomorphy, and myomorphy. These variations of the zygomasseteric system, and the assumption that each evolved only once, have historically been used as the primary criteria for defining rodent systematics and understanding rodent evolutionary patterns (e.g., Brandt, 1855; Miller and Gidley, 1918; Simpson, 1945; Wood, 1955). These approaches have come under scrutiny as the complex evolutionary history of the rodent zygomasseteric system has begun to be better understood (e.g., Wood, 1965; Huchon et al., 2002; Adkins et al., 2003; Blanga-Kanfi et al., 2009; Cox et al., 2012; Patterson and Upham, 2014).

A primary consideration of this study is interpreting the independent acquisition of these zygomasseteric systems by different groups, thereby resulting in polyphyletic assemblages

according to traditional approaches. Protrogomorphy is clearly the primitive condition for rodents. The only extant rodents with this condition are *Aplodontia rufa* (the mountain beaver)—the lone surviving member of a group of protrogomorphous rodents (Aplodontoidea)—and the African Bathyergidae and Heterocephalidae. *Aplodontia* has been historically described as the most primitive living rodent (e.g., Arjo, 2007), but protrogomorphy in this taxon is now regarded as case of secondary acquisition of the primitive state (i.e., Druzinsky, 2010). Bathyergids were recognized for their unique zygomasseteric system in early attempts to classify rodents (Tullberg, 1899), and most workers preferred to consider them as protrogomorphs modified from hystricomorphs (e.g., Maier and Schrenk, 1987). Micro-CT study has documented the protrogomorphous condition in *Heterocephalus glaber* (Cox and Faulkes, 2014). Schmerge and Martin (in review) described a genus of palaeocastorine beaver, *Paraeuhapsis*, that is also protrogomorphous.

The arrangement of the cranial muscles that characterize *Paraeuhapsis* is described in this paper. The perspective that protrogomorphy was a primitive condition later abandoned by most rodent lineages has limited attempts to understand the functional significance of the protrogomorphous state in such burrowing taxa as *Aplodontia*. The sites for muscle attachment and the subsequent organization of the cranial musculature in *Paraeuhapsis* is described and compared to other extant and extinct rodents in this paper, including the complex of masseter, temporalis, and specialized lip-closing muscles.

Paraeuhapsis was recognized, in part, on the basis of its relatively deepened rostrum. The rostrum of *P. ellicottae* is even further adapted from *P. breugerorum* in the modification of its nasal bones. The nasals are bowed upward, bear a small boss at the symphysis, and display tremendous rugosity visible to the naked eye. Martin (1987), in his original description of the

specimen later redescribed as *P. ellicottae*, noted this rugosity as evidence for the presence of either a keratinous nose pad (rhinarium) or potentially a nasal horn. Thickening of the nasal dermis is common in burrowing rodents (Stein, 2000), although the most prominent nose pads are known in the genus *Spalax* (Nevo, 1999). Among rodents, facial horns are known only in mylagaulids, a group closely associated with the aplodontids, making the potential acquisition of a horn in *Paraeuhapsis* a clear case of convergent evolution. The integumentary structure of the euhapsine beavers *Euhapsis* and *Paraeuhapsis* is investigated using epi-illumination microscopy to study the surface texture of the nasal bones and micro-CT scanning to interpret the internal bone porosity. The potential occurrence of a keratin fiber horn in *Paraeuhapsis* and its potential function in burrowing behavior is discussed.

MATERIALS AND METHODS

The holotype of *Paraeuhapsis ellicottae* (KUVP 48015) was micro-CT scanned at the University of Missouri-Kansas City School of Dentistry. Micro-CT scanning was performed on a vivaCT 40. Scans were performed at 55 kV and 145 μA. CT scans were generated with a slice increment of 19 μm and a resolution of 19 μm per voxel.

Surface photographs of rodent nasal bones were taken using an AD413TA-12V Dinolite epi-illumination microscope. The nasal bones of extant *Geomys bursarius* (KU BAS 12), *Nannospalax leucodon* (KU 102078), and *Tachyoryctes splendens* (KU 41126) were examined for the purpose of associating nasal bone texture with known keratinous soft structures in subterranean rodents. The identity of openings (vascular, Sharpey's fiber attachment, pathology, etc.) in the nasal bones was interpreted based on Rothschild (2013). The nasal bones of the extinct palaeocastorines *Euhapsis martini* (AMNH 10818), *Paraeuhapsis breugerorum* (KUVP

28376), *Paraeuhapsis ellicottae* (KUVP 48015) and the mylagaulids *Pterogaulus laevis* (KUVP 9808) and *Ceratogaulus minor* (KUVP 6886) were examined to interpret the potential nasal structures based on comparison to the observed extant rodents. Photographs were taken of the frontal bones in the rhinoceros *Diceros bicornis* (KU 142370) using a Panasonic DMC-TZ5.

The skull in Figure 1 is a composite reconstruction. The cranium is based on KUVP 48015 (*Paraeuhapsis ellicottae*), in which the zygoma are largely absent. The zygomatic arches were reconstructed based on comparisons within the euhapsines *Euhapsis martini* (AMNH 10818) and *E. platyceps* (CM 1220). The mandible was drawn based on KUVP 28376 (*P. breugerorum*). The fit of the mandible and cranium of the two species is good, but has some imperfections worth noting. The overall tooth wear of KUVP 48015 and KUVP 28376 does not match ideally. This could be due to slightly different chewing patterns (and diets). This could also relate to a difference in the ontogenetic ages of the specimens, as the lengths of the tooth rows are consistent, and the overall proportion of the mandible fits well to the cranium.

Institutional abbreviations—**AMNH**, American Museum of Natural History, New York NY; **CM**, Carnegie Museum, Pittsburgh, PA; **KU**, University of Kansas Mammalogy Division, Lawrence, KS; **KUVP**, University of Kansas Vertebrate Paleontology Division, Lawrence, KS.

Nomenclature

The primitive mammalian masseter muscle is divided into two primary muscle bodies, referred to as the superficial and deep masseter. There is some confusion in terminology used to describe the masseter musculature of rodents, because the masseter muscle is further differentiated into an additional layer in rodents (Fig. 1). The medial layer, which is differentiated into two muscle bodies (anterior and posterior) in rodents, is variously referred to

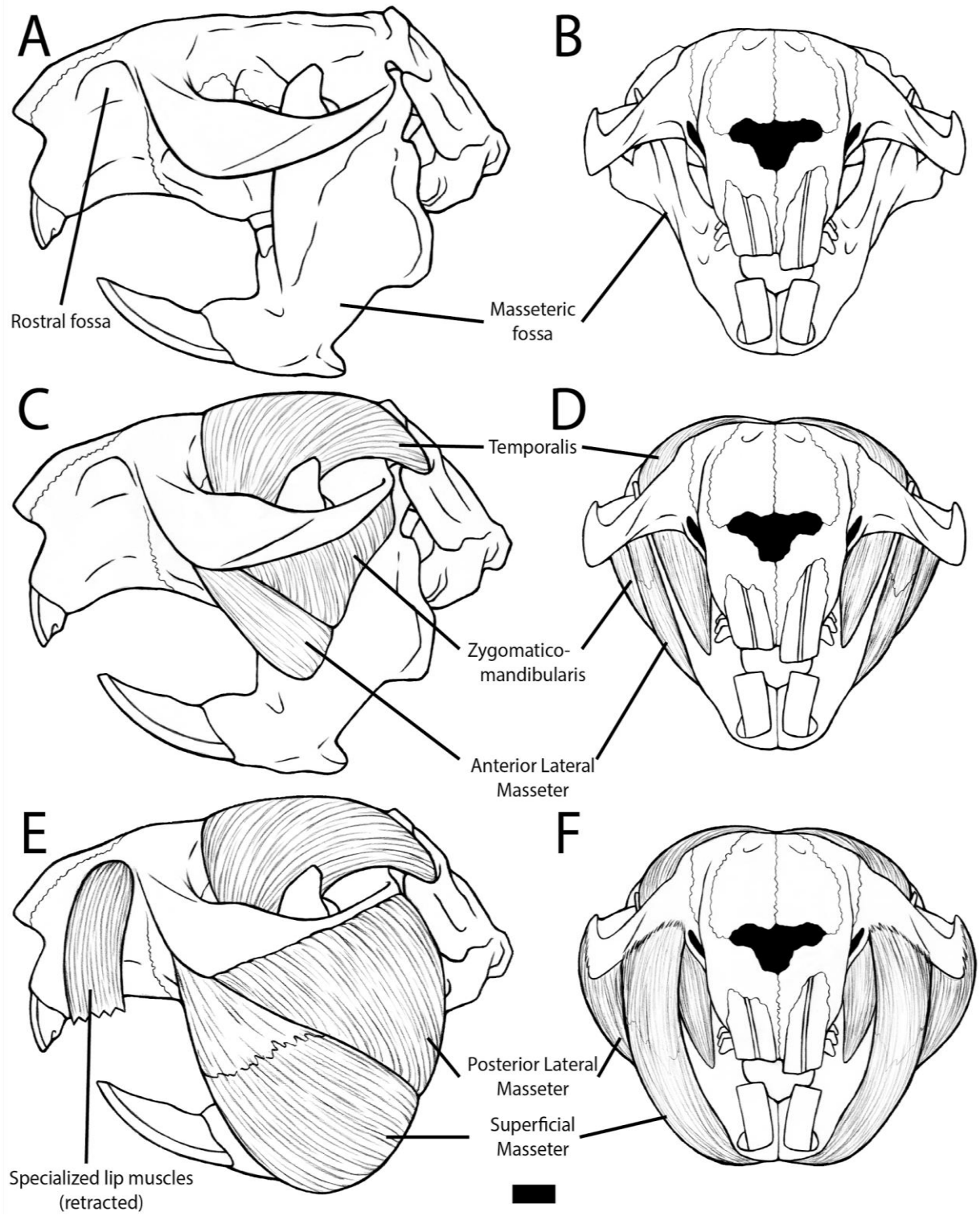
A
B
Rostral fossa
Masseteric fossa
C
D
Temporalis
Zygomatico-mandibularis
Anterior Lateral Masseter
E
F
Posterior Lateral Masseter
Superficial Masseter
Specialized lip muscles (retracted)

Figure 1—*Paraeuhapsis* cranial muscles reconstruction. Cranium illustrated from the holotype of *P. ellicottae* (KUVP 48015), mandible illustrated from the holotype of *P. breugerorum* (KUVP 28376). Scale bar 5 mm. (A) Lateral view of reconstructed composite skull. (B) Anterior view of reconstructed composite skull. (C) Reconstruction of deep masseter musculature and temporalis, lateral view. (D) Reconstruction of deep masseter musculature and temporalis, anterior view. (E) Reconstruction of superficial masseter musculature and temporalis, lateral view. Specialized lip-closing muscle placement is approximated and illustrated as reflected and cut from presumed soft tissue insertion sites. (F) Reconstruction of superficial masseter musculature, anterior view.

as the lateral masseter (e.g., Druzinsky, 2010; Druzinsky et al., 2011) or the deep masseter (e.g., Cox and Jeffery, 2011). The deepest layer is then variously referred to as the zygomaticomandibularis (e.g., Druzinsky, 2010; Cox and Jeffery, 2011) or the deep masseter (as for most mammals, e.g., Ball and Roth 1995; Thorington and Darrow, 1996). The deepest layer is occasionally differentiated into two muscle bodies (e.g., Druzinsky, 2010); the larger anterior muscle mass is referred to as the zygomaticomandibularis (ZM), and the posterior muscle mass is referred to as the posterior masseter (PM). The PM is diagnosed in wet specimens by the isolation of muscle fibers into a distinct body, but is not reliably diagnosed by muscle scars on the bone, and therefore is not discussed in this study. We use the nomenclature of Druzinsky et al. (2011) for clarity and will only use the term 'deep' in the anatomical sense to refer to position of one muscle relative to another.

We use several terms to describe the texture of the bones. The term rugosity is a term used to describe the surface texture of the bone. This term is applied to roughened bone that

displays either a dense concentration of neurovascular openings or attachment sites for integument via cartilage, also referred to as muscle scarring. We use the term rugosity to refer collectively to this appearance and then will qualify specific differences as they relate to distinct features. The term porosity is used to describe apertures visible in cross-section via micro-CT scanning.

RESULTS

Cranial morphology of Paraeuhapsis

The cranium of *Paraeuhapsis* is marked by several significant features (Fig. 1). There is a prominent sagittal crest, and the temporal bones are noticeably rugose. The rostrum is marked by a deep depression on the lateral sides, a character of the tribe Euhapsini (Martin, 1987; Schmerge and Martin, in review). *Paraeuhapsis* is unique, however, in comparison to other euhapsines in the placement of the infraorbital foramen below the zygomatic arches rather than on the rostrum proper (Fig. 2). The infraorbital foramen is thin and slitlike, and the masseteric tubercle is highly reduced. The anterior portion of the zygomatic arch is modified into a plate as in other castorids, but the fossa formed along the plate to accommodate the masseter does not extend onto the rostrum (Fig. 2 C).

Mandible Morphology of Paraeuhapsis

The angular process of the mandible is strongly laterally deflected, and the articular process is a medially deflected from the coronoid process. This condition was described as

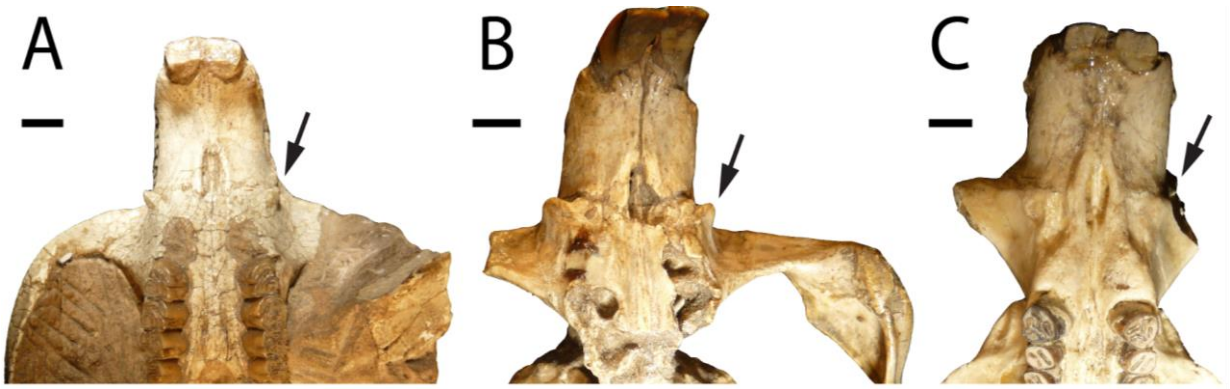

Figure 2—Stepwise evolutionary reduction and elimination of the rostral attachment of the masseter muscle in euhapsine rodents. Arrows point to the masseteric tubercle. Scale bars 5 mm. (A) *Euhapsis martini*, with an enlarged masseteric tubercle typical of sciuromorph rodents. (B) *Euhapsis platyceps*, in which the masseteric tubercle is shifted somewhat posteriorly and is angled upward. (C) *Paraeuhapsis ellicottae*, with a diminished masseteric tubercle ventral to the zygoma. The anterior zygomatic fossa does not extend onto the rostrum, and the origin of the superficial masseter is therefore restricted to the zygoma in *Paraeuhapsis*, creating a protrogomorphic arrangement.

hystricognathy by Martin (1987), but is clearly distinct from the hystricognathous condition seen in living members of the Hystricognathi (e.g., Korth, 1994; Schmerge and Martin, in review). The masseteric fossa is broad and extends across the angle and ramus. There are several pocketlike subdivisions formed in the masseteric fossa that correspond to the insertions of the separate divisions of the masseter (see Fig. 1 A, B). These pockets are depressions within raised rims of bone and have a somewhat roughened texture. There is a deep pocket along the angle of the mandible, and another pocket formed on the medial aspect of the ascending ramus posterior to the toothrow.

Structure of the nasal bones

The texture of the nasal bones of several burrowing rodents is presented in Figure 3. Rodents with diminutive noses (e.g., *Geomys, Tachyoryctes*) possess constricted nasal bones with smooth surface textures (Fig. 3 A, B). Many rodents of the family Spalacidae bear an enlarged nose or rhinarium. *Nannospalax leucodon* has an enlarged rhinarium, which is reflected in the structure of its nasal bones as a roughened anterior portion with rugosity created by the attachment of Sharpey's fibers (Fig. 3 C) and a smooth posterior portion. The nasals of *Nannospalax* are more rugose than those of the other examined extant rodents. *Nannospalax* possesses wide nasal bones that bow the premaxillae outwards.

The nasal bones of *Euhapsis martini*, an extinct palaeocastorine beaver from the late Oligocene, have a greater degree of rugosity than any living rodent (Fig. 4 A). The rugosity is characterized by a series of slightly to highly ellipsoid openings that appear to be surrounded by rings of bone growth. There is no pattern in the variability of the opening size and shapes, and the pattern of rugosity is furthermore consistent across the entire surface of the nasals. The pattern of rugosity of *Euhapsis* is overall similar to that of *Nannospalax*, but differs only in the relative size and extent of the openings in *Euhapsis*. The nasal bones are widened, and the premaxillae bowed outward in a way reminiscent of *Nannospalax*.

The nasals of *Paraeuhapsis ellicottae* are the most unique of all the investigated rodents. They exhibit much greater rugosity overall compared to other rodent nasal bones examined (Fig. 4 B), including those of *E. martini*. The anterior portion of the nasals bears a low, elongate boss. The boss is characterized by fine-scale rugosity and is surrounded entirely by an annular zone of increased rugosity. The annular zone is marked by a greater frequency of openings and more elongate and larger openings, which is visible on the surface (Fig. 5) and in cross-section (Fig.

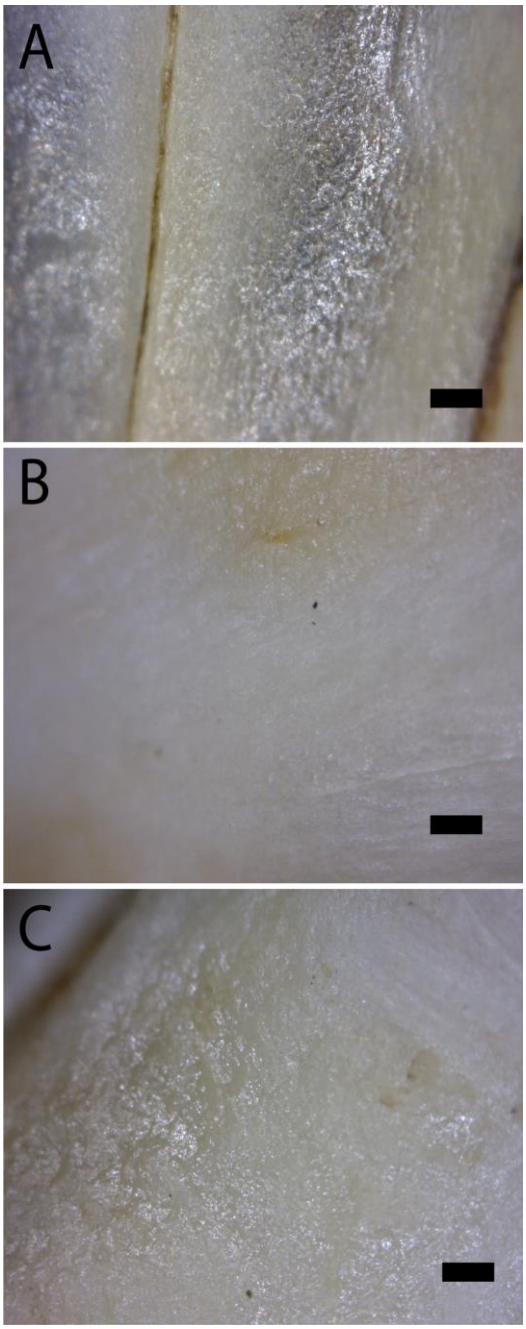

Figure 3—Surface rugosity of the nasal bones of burrowing rodents. Sharpey's fiber insertions are circular openings within concentric rings of bone. Overall rugosity low in (A) *Tachyoryctes splendens* (KU 41126) and (B) *Geomys bursarius* (KU BAS 12). There are widespread Sharpey's fiber insertions across the anterior nasal region in (C) *Nannospalax leucodon* (KU 102078). Scale bar 100 microns.

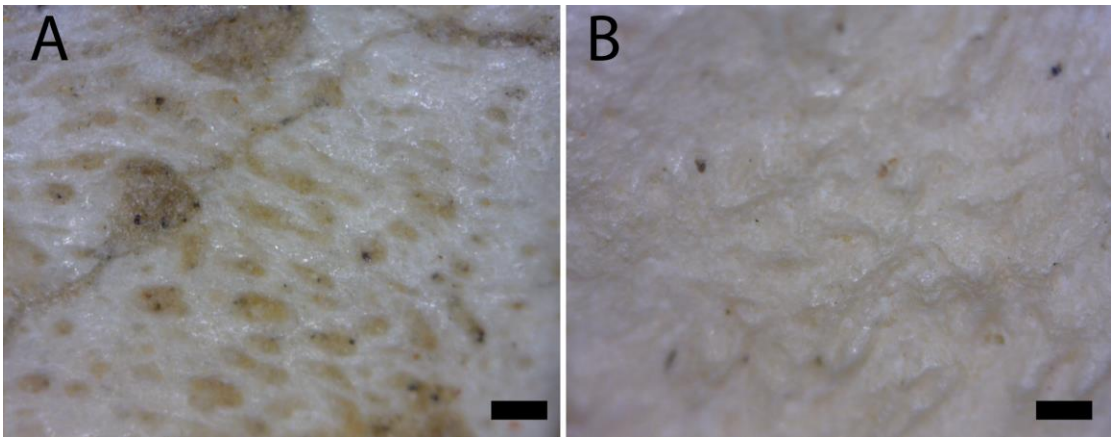

Figure 4—Surface rugosity of the nasal bones in extinct subterranean rodents. (A) Rugosity in *Euhapsis martini* (AMNH 10818) appears as ellipsoid openings surrounded by bony rings. (B) Rugosity in *Paraeuhapsis ellicottae* (KUVP 48015) appears as deep furrows. Scale bar 100 microns.

6). The nasals are overall much thicker than in any of the other rodents examined. The nasal bones are wider than those of the other investigated rodents, and they bow the premaxillae out considerably.

Micro-CT scanning revealed differential porosity in the nasal bones of *Paraeuhapsis*. The boss can be seen as an elevated region relative to the rest of the nasals in cross section. The boss is furthermore characterized by only fine-scale porosity (outlined in red in Fig. 6 C, D). The surrounding annular zone can be seen in cross section as a zone of increased pore frequency and size (zone outlined in blue in Fig. 6 C, D). The annular zone of porosity is then surrounded by dense bone that displays only a limited degree of porosity. This zone becomes larger in the posterior portion of the nasals (Fig. 6 D).

DISCUSSION

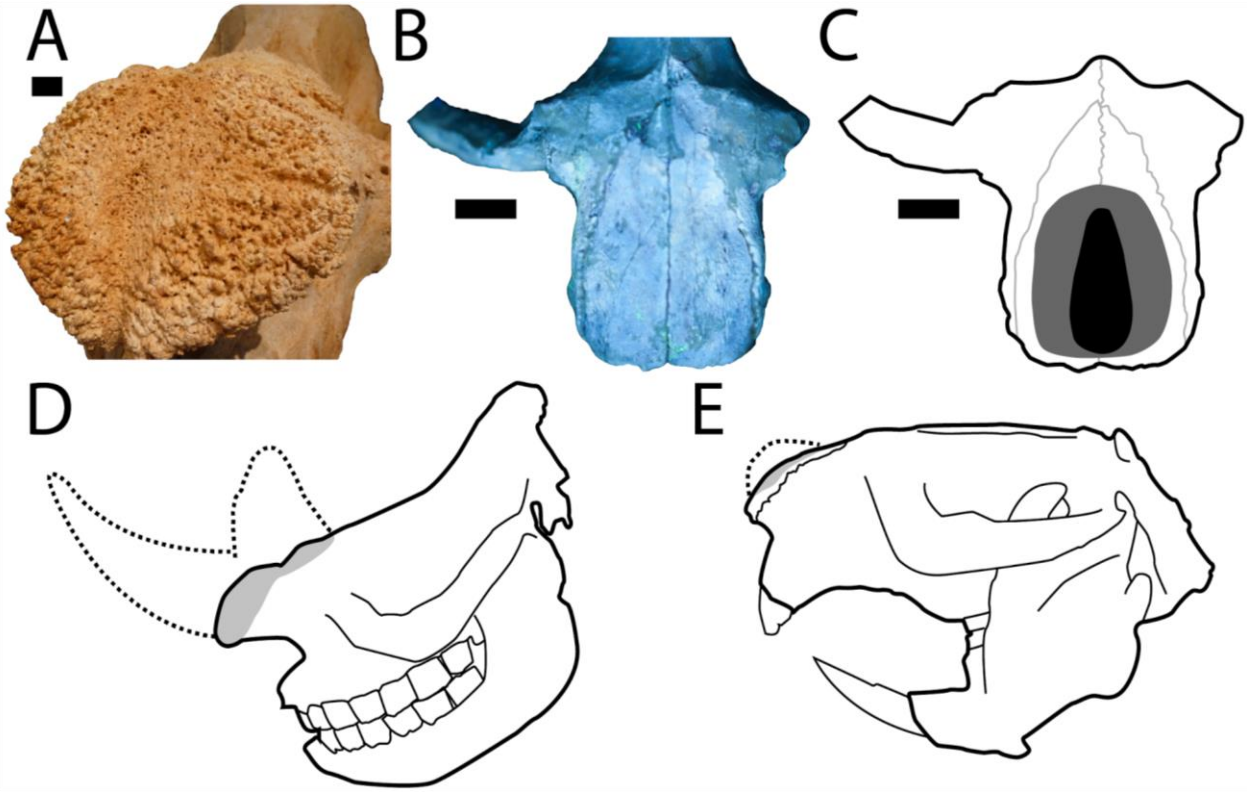

Figure 5—Comparison of the nasal rugosity and horn morphology of a rhinoceros to that of *Paraeuhapsis*. (A) Dorsofrontal view of *Diceros bicornis* (KU 142370). Outer annular zone of high rugosity surrounds inner zone of comparatively low rugosity. Scale bar 1 cm. (B) *Paraeuhapsis ellicottae* (KUVP 48015), photographed under UV light. Scale bar 5 mm. (C) Interpretative illustration indicating outer annular zone of high rugosity (gray) and inner zone of comparably lower rugosity associated with the nasal boss (black). Scale bar 5 mm. (D and E) Relationship of the zone of annular rugosity, shaded in gray, to the attachment zone of the keratin fiber horn in (D) *D. bicornis*, compared to the hypothesized horn placement in (E) *P. ellicottae.*

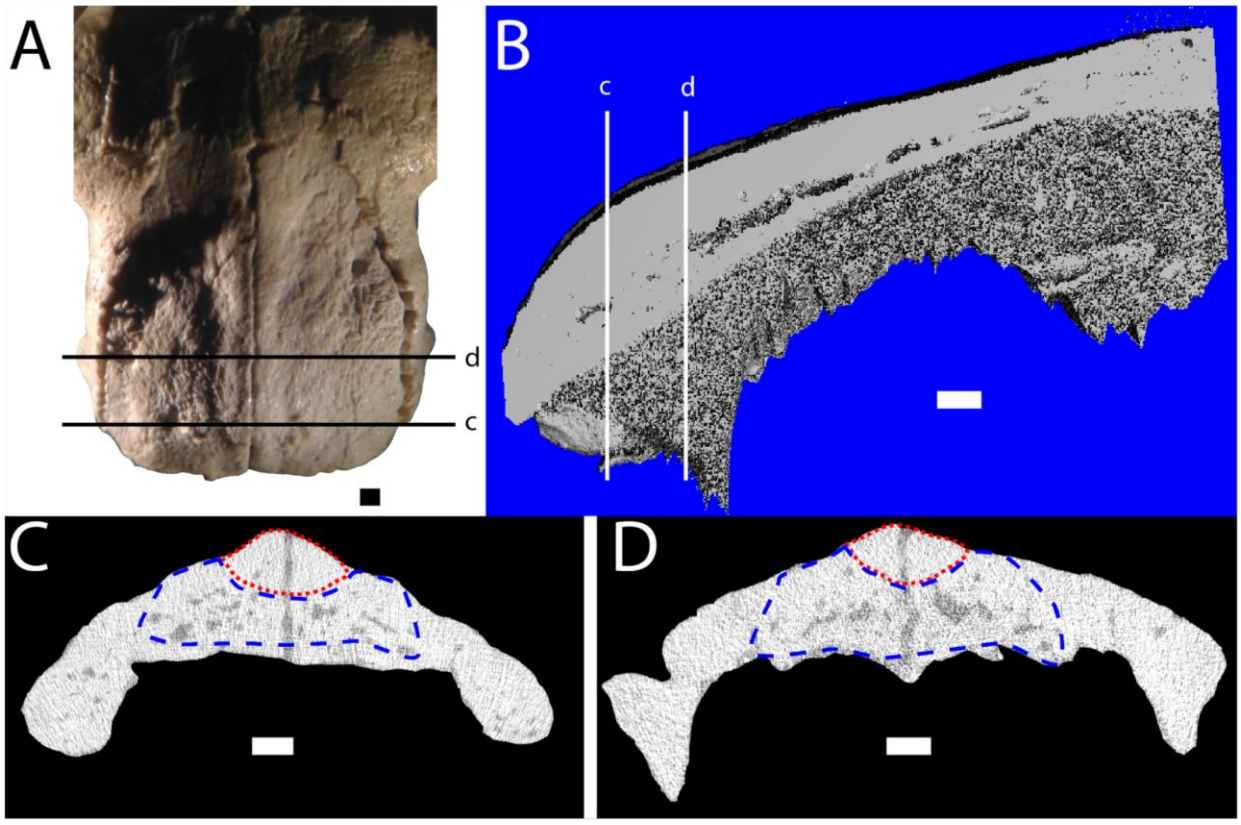

Figure 6—Nasal porosity in *Paraeuhapsis*. Scale bar 1 mm. (A) View under white light. Lines c and d indicate positions of coronal slices shown in (C) and (D), respectively. (B) Parasagittal section taken from the integrated micro-CT volume, illustrating enlarged openings in the nasal vascular network and the nasal cartilage. Rough texture below the solid gray zone correponds to matrix in the nasal cavity. (C) Coronal section from the micro-CT. Nasal boss is a low porosity zone (outlined in red, short dashes) surrounded by a high porosity zone (outlined in blue, long dashes). Porosity of the surrounding maxilla is also higher, suggesting a possible site of attachment for a rhinarium. (D) Coronal section from the micro-CT, colored and dashed lines as in (C).

Cranial Muscles of Paraeuhapsis

The temporalis muscle of *Paraeuhapsis* is a comparatively enlarged muscle relative to most rodents. The height of the sagittal crest, the broadened and rugose attachment sites for the muscle, the interorbital constriction, and the deepening of the fossa on the medial face of the ascending ramus are osteological correlates of an emphasized temporalis. The temporalis only comprises about 10% of the cranial muscle mass in a typical sciuromorph (i.e., *Sciurus*; Cox and Jeffery, 2011), but that mass was likely greater in *Paraeuhapsis* given the increased space for attachment.

The pits on the rostrum are likely the origin sites for a specialized series of lip closing muscles. These muscles almost certainly facilitated lip closure during burrowing activity in order to keep soil out of the oral cavity. The position of the pits are also reminiscent of the pits possessed by geomyoids (e.g., *Geomys*) that anchor the retractor muscles for the cheek pouches, which are used for food storage and transport. Without soft tissue preservation, this hypothesis is difficult to consider presently, but this possibility should be investigated further.

The masseter complex in *Paraeuhapsis* is quite unique. The ZM is a relatively minor component of the masseter musculature. It has a broad insertion in a deep pocket on the lateral surface of the mandible (Fig, 1 C, D). The ZM in modern rodents originates on the alisphenoid and the internal surface of the zygoma, but the absence of the squamosal bones from all known specimens of *Paraeuhapsis* requires speculation as to the exact size of this muscle. The anterior lateral masseter originates on the zygoma and inserts into a small pocket on the lateral surface of the mandible, anterior to the insertion of the ZM. The posterior lateral masseter inserts across the angle of the mandible and originates from the lateral portions of the squamosal bone. The superficial masseter is one of the two largest individual muscle bodies of *Paraeuhapsis*. The

origin of the superficial masseter of *Paraeuhapsis* is restricted entirely to the zygoma, in a crescent-shaped fossa on the anterior and ventral portion of the zygomatic plate (see Fig. 1 A, C). The superficial masseter then inserts broadly over the lateral surface of the mandible, extending between the incisor alveolus and approximately the midsection of the mandible (see Fig. 1 C).

Euhapsine rodents underwent a stepwise transformation from sciuromorphous forms into protrogomorphous forms (see Fig. 2). *Euhapsis martini* (see Fig. 2 A) and *E. platyceps* (see Fig. 2 B) are both modified sciuromorphs. *Euhapsis martini* has a diminished masseteric tubercle that is shifted somewhat posteriorly compared to other sciuromorphs, but it still remains prominent on the rostrum. The infraorbital foramen in *E. martini* was compressed, and transmitted only a small portion of the masseter (if any). The infraorbital foramen in *E. platyceps* is tilted upwards, so even though it appears as if the masseteric tubercle is relatively shifted forward, the attachment of the superficial masseter is shifted posteriorly on the skull compared to the arrangement in *E. martini*. The infraorbital foramen and masseteric tubercle are shifted below the zygomatic arch in *Paraeuhapsis* (Fig. 3 C). The superficial masseter no longer attaches to the rostrum, and, therefore, *Paraeuhapsis* is protrogomorphous.

All extant rodents, except *Aplodontia rufa* and the bathyergoids, have modified the masseter musculature to extend onto the rostrum. Aplodontids display a modified version of the primitive protrogomorphous condition, which has been secondarily reacquired (Druzinsky, 2010). In all nonprotrogomorphs, the superficial masseter is extended onto the rostrum. The sciuromorph condition is formed by the attachment of the anterior lateral masseter to the rostrum and the anterior surface of the zygoma in a broad sulcus anterior to the zygomatic plate. Hystricomorph rodents instead have extended the ZM through the infraorbital foramen onto the rostrum, leaving the lateral masseter undifferentiated and restricted to the posterior portion of the

zygoma (Cox and Jeffery, 2011). Myomorph rodents are generalists that extend both the lateral masseter and the ZM onto the rostrum (Cox and Jeffery, 2011). The diminished size of the average rodent temporalis muscle mass, in concert with the rostrally expanded masseter musculature, serves the purpose of directing the bite force primarily in the antero–posterior direction (Druzinsky, 2010). The elimination of the rostral portions of the masseter muscle and the enlargement of the temporalis muscle in *Paraeuhapsis*, therefore, relates to an increase in the power of the dorso–ventral bite force.

There appears to be a link between subterranean lifestyles and protrogomorphy. Bathyergoids were once grouped into their own superfamily (Bathyergomorphi; Tullberg, 1899) or their own suborder (Bathyeromorpha; Wood, 1955) based on their unique combination of a protrogomorphous skull and a hystricognathous jaw. Though this classification fell out of favor, bathyergids are notable for their unique zygomasseteric system, though it likely is derived from the hystricomorphous state based on their somewhat enlarged infraorbital foramen. *Aplodontia* has been suggested to be a head-lift digger based on its skull shape (Samuels and Van Valkenburgh, 2009) and observations of captive specimens (Druzinksy, 2010), though its burrowing behaviors in the wild are not well described. Nevertheless, many prolific burrowers make use of a protrogomorphic skull configuration, as evidenced by the occurrence of protrogorphomorphy in aplodontoids and bathyergoids. This is potentially related to the need to widen the gape (Cox and Faulkes, 2014)—an explanation supported by the development of the secondary glenoid in *Paraeuhapsis* (Schmerge and Martin, in review). The relatively increased mass of the temporalis muscle, associated with the development of this secondary protrogomorphy, has also been associated with an increased bite force at the incisors (Cox and

Faulkes, 2014). This enhanced bite force would dramatically increase the biting efficiency during incisor digging.

Integumentary Structure of the Nasals

Epi-illumination microscopy can reveal the nature of integumentary connections with the periosteum (not preserved in fossils) and bone. Sharpey's fibers (Sharpey et al., 1867) can be recognized microscopically on the surface of bone as round apertures surrounded by bony rings (Rothschild, 2013). The occurrence of Sharpey's fibers is indicative of the presence of tissue that is tightly bound to the bone, generally teeth (in the oral cavity), muscles (via ligaments), or integumentary structures (Aaron, 2012).

Euhapsis martini is one of the early members of the beaver tribe Euhapsini, a clade that diverged from the remaining palaeocastorine beavers into head-lift-digging behavior (Martin, 1987; Schmerge and Martin, in review). The surface of the nasal bones in *Euhapsis* resembles most strongly the nasal bones of *Spalax* and *Nannospalax*, two well-known head-lift-digging rodents (Hildebrand, 1985). Many modern burrowing rodents have somewhat enlarged and flattened noses used in packing soil and valvular external nares that prevent soil from entering the nasal cavity (e.g., Jarvis and Sale, 1971). Rodents of the subfamily Spalacinae, such as *Spalax* and *Nannospalax*, bear a rhinarium (Klauer et al., 1997; Nevo, 1999). Hildebrand (1985) demonstrated that the nasal bones of burrowing species bearing a rhinarium are thickened. The rhinarium of these taxa assist in the movement of soil during burrowing and are an additional means to block soil from the nasal passages. The interpretation of a rhinarium on the rostrum of *E. martini* is reasonable given the increased width of its nasal bones, the microscopic rugosity of

the nasals, and the presence of Sharpey's fiber insertions throughout the nasal bones (see Fig. 4 A).

The nasal bones of *Paraeuhapsis* are highly modified compared to *Euhapsis* and all other living subterranean rodents. At a minimum, these differences correspond to a relatively enlarged rhinarium, but the nasals of *P. ellicottae* would likely have supported a large integumentary structure. The arrangement of a somewhat rugose boss surrounded by an annular zone of greater rugosity—visible even to the naked eye—is highly similar to the nasal textures of living horned rhinoceroses (see Fig. 5 A).

Rhinoceroses possess horns unique from all other living mammals. Horns are keratinous tissue and are in the strict sense not made of bone, though many horns sheathe a bony process (i.e., core). Three distinct types of horns are known in living mammals: 1) keratin fiber horns, in rhinoceroses; 2) paired, symmetrical horns with a permanent bony core, in bovids; and 3) paired, symmetrical horns with a permanent bony core and a deciduous sheath, in antilocaprids (Hall, 2005). Horns are distinct from antlers in cervids, which are fast-growing, branching deciduous structures derived from bone and covered with a thin epidermal layer (i.e., velvet) during the growth period, and ossicones in giraffes, which are bony knobs covered in a thin layer of highly vascularized skin (Hall, 2005). Horns with bony cores occurred independently in some fossil groups, namely the Eocene titanotheres and the Miocene mylagaulids. The keratin that forms horns is structurally similar to the alpha keratin of horse hooves and whale baleen (Hall, 2005).

The keratin of rhinoceros horns grows from the dermis below and not from the bone itself. The dermal layer, which ranges from 1–2 cm thick, is anchored to the nasal and frontal bones by Sharpey's fibers (Hieronymus, 2009). The keratin of the horn is intermingled with the dermis, and the horn, therefore, grows in layers (laminae) with the shape of the horn being

produced by the morphology of the keratin fibers in the horn and environmental wear (Hieronymus et al., 2006).

Interpretation of nasal horns in fossil rhinoceroses (and consequent sexual dimorphism of certain species) is controversial. The horn morphology of some extinct taxa (i.e., the wooly rhinoceros, *Coelodonta antiquatis*) is known with certainty from Paleolithic art and rare occurrence of horns found in permafrost or bogs (Fortelius, 1983; Prothero and Schoch, 2002). Interpretation of the presence of a horn in a fossil taxon, at a minimum, depends on the occurrence of rugosity on the surface of the nasal bones and the architecture of the nasal becoming thickened, bowing upwards, and containing a boss (figure 2.4 of Prothero, 2005). Refinement of this approach indicates that the rugosity must be variable, with an outer ring of greater rugosity indicating the site of the attachment of the modified dermis to the bone, and an inner zone of finer rugosity characterized by the presence of nutritive foramina for the horn tissue (Hieronymus, 2009). The nasal bones of *Paraeuhapsis ellicottae* meet all of these criteria (see Fig. 5). Epi-illumination microscopy of the nasal bones of *P. ellicottae* reveals texture consistent with attachment to an integumentary structure. The horn-supporting portions of the nasal bones of modern rhinos (e.g., *Diceros bicornis*) consist of a ring of Sharpey's fibers surrounding a vascularized zone that contains the nerves and blood supply to the horn (see Fig. 5; Hieronymus et al., 2006; Rothschild, 2013). The nasal bones of *Euhapsis martini* contrast with those of *P. ellicottae* by possessing numerous diffuse Sharpey's fibers throughout the anterior of the nasals (see Fig. 4). This is consistent with an interpretation of a broad rhinarium on the rostrum of *E. martini*; likewise, the rhinarium of modern *Spalax* is thick and strongly set into the nasal cartilage (Klauer et al., 1997). The rugosity and restricted occurrence of Sharpey's fibers in *Paraeuhapsis*, however, is analogous to the pattern seen in the nasals of horned rhinoceroses.

The single nasal horn of *Paraeuhapsis* contrasts with the paired horns of mylagaulids in several ways. Two genera of mylaugalids, *Ceratogaulus* and *Mylagaulus*, possess paired bony horn cores on the rostrum (Hopkins, 2005; Czeplewski, 2012). Paired horns are unique among rodents to the mylagaulids. The horns of mylagaulids have a bony core and would have been covered in a keratinous sheath during life. This type of horn is most similar to the horns of bovids (e.g., *Bison*) rather than the keratin fiber horn of *Paraeuhapsis*. The morphology of the horn is subject to interpretation (Fig. 7), as its presence can only been inferred based on the structure of the nasal boss, and there is no evidence of its outline. The cross-sectional area of the horn was likely longer than it was wide, based on the relative dimensions of the nasal boss (see Fig. 5). The horns of mylagaulids were paired, typically round to ellipsoid in cross-section, straight, conically shaped, and diverged from the midline as they grew upward. The single horn of *Paraeuhapsis* may likewise have grown straight and vertically, though the keratinous horns of living rhinoceroses have some curvature associated with them as they grow. The morphology of the horn would depend on its growth rate, its unique keratin structure, and its usage. The horn of *Paraeuhapsis* would likely have been a blunted structure that was wider in its area than it was tall if it was used often in burrowing behaviors.

Horn Function

The function of mylagaulid horns has been the subject of previous discussion. Gidley (1907) and Fagan (1960) originally attributed the horns to burrowing. Other posited functions have been defense, species identification, and sexual combat (Hopkins, 2005), with defense being the preferred explanation. A major argument against the use of horns for burrowing in

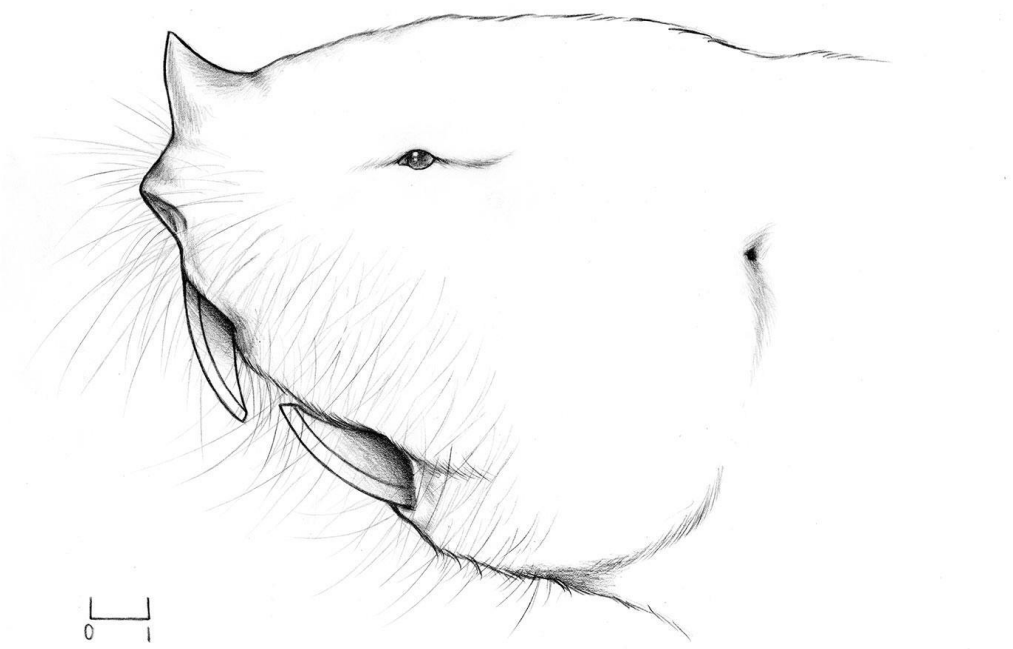

Figure 7—Life reconstruction of *Paraeuhapsis*.

mylagaulids was the placement of the horns; Hopkins (2005) argued that the horns were placed too far back on the skull to exert mechanical advantage within the confined space of a burrow.

The debate over the function of horns in mylagaulids likely ignores several important evolutionary contingencies. That the most derived members of the genera *Ceratogaulus* and *Mylagaulus* evolved horns independently remains a possibility, but these taxa likely did not evolve large horns with bony cores without an intermediate form. If *Paraeuhapsis* did in fact possess a horn, there are several taxa of mylagaulids previously interpreted as hornless and bearing nasal bosses (e.g., *Pterogaulus*) that may also have possessed horns. The bosses in these mylagaulids are positioned near the anterior end of the nasal bones, in a place where there was

likely mechanical advantage for burrowing in soil in a way related to head-lift digging. The origin of bony horns in mylagaulids could potentially be from ancestors that possessed keratinous horns.

The environmental factors that shaped these organisms are of even further importance. Though they are separated in time, *Paraeuhapsis* and the horned mylagaulids both lived in comparatively cool and dry habitats (Martin and Naples, 2002), which suggest they had to cope with similar environments. Martin and Meehan (2005) documented patterns of convergent evolution in mammalian faunas owing to cyclic changes in climate. *Paraeuhapsis* and horned mylagaulids both flourished during the terminal parts of their respective climate cycles (i.e., C cycles), indicating that a horned rodent ecomorph may correlate with a certain set of climate and environmental parameters as do scimitar- and dirk-tooth sabertooth feliforms (e.g., Martin, 1980; Martin and Meehan, 2005)

Paraeuhapsis, and most of the other euhapsine beavers, likely employed a head-lift-digging strategy for burrowing in the ground based on the morphology of its skull and teeth (Samuels and Van Valkenburgh, 2009; Schmerge et al., in review). The morphology of its skull, in addition to being highly convergent on living subterranean rodents, is completely unsuited for the lifestyle of a surface-dwelling rodent. The orbits of all euhapsines were small, and the external pinnae were likely small, thereby severely limiting the ability to detect predators in an aboveground setting. The mylagaulid *Ceratogaulus* almost certainly could not have survived on the surface; its eyes faced upward and its limbs were clearly adapted to manipulating soil rather than moving along the ground. Even if the bony horns of *Ceratagaulus* were most useful for defense purposes, it likely used them in the confines of a burrow, similar to how a badger positions itself near the opening of its den (Nowak, 1999). The postcranial skeleton of

Paraeuhapsis is only poorly known, but is likely convergent on the form of horned mylagaulids. The horn *Paraeuhapsis* possessed could not have functioned in a defensive purpose on the surface, as any predator would overtake it before it could bring the horn to bear. Sexual combat and species identification are possibilities, but the sexual combat hypothesis cannot be tested without trace-fossil evidence, and the species identification hypothesis cannot be tested without knowing the morphology of the horns. The species identification hypothesis is not preferable given their likely subterranean behavior. A digging function is, therefore, most preferable, given the other skeletal correlates for head-lift-digging behavior in *Paraeuhapsis*.

We are unable to determine the precise function of the horn in burrowing activity without trace-fossil evidence (e.g., Martin and Bennett, 1977; Gobetz, 2006). Extant subterranean rodents use three different burrowing strategies to dig through the soil: scratch digging with the manual claws, chisel-tooth digging with the incisors, or head-lift digging using the incisors and the head together as a twisting shovel (Hildebrand, 1985; Nevo, 1999; Stein, 2000). These behaviors have been interpreted in palaeocastorine beavers using morphometric analysis of the skull, though many euhapsine beavers plotted outside the known morphospaces for these behaviors (Samuels and Van Valkenburgh, 2009). The possibility remains that some of these beavers were using a burrowing strategy not employed by living rodents, which is a strong possibility given the absence of horned rodents in modern fauna. The pronounced correlation of the skull shape of *Paraeuhapsis* with head-lift digging does suggest at least some basic similarity to living head-lift diggers, so this remains a reasonable conclusion. *Paraeuhapsis* most likely used the powerful bite created by its enlarged temporalis muscles to assist in breaking soil loose and used its horn to sweep aside the loosened soil, based on knowledge of living burrowing rodents. The horn was not likely the primary tool for breaking soil loose. The incisors function much better as scrapers

in resistant soils because of the hardness of enamel, and keratin is favored in the claws of scratch diggers because of its ability to flex with pressure (Hildebrand, 1985). Since a keratin fiber horn would not flex like a claw, the horn would likely wear too quickly to be the primary or singular burrowing tool. We cannot rule out a secondary function of the horn in burrowing, but the horn at least would serve to clear soil once it was broken free. Additional work should be undertaken to understand the function of horns in this taxon.

There are two possible hypotheses to explain the reacquisition of the protrogomorphous state in *Paraeuhapsis*: 1) the increasingly broad rhinarium must be accommodated by the retreat of the masseter to the zygoma; or 2) the possible emphasis on horn digging in these taxa results in a simultaneous reduction of incisor procumbency, which ultimately results in a protrogomorphous condition. There remains also the possibility that both of these explanations play a role in the acquisition of protrogomorphy. The maxilla of *P. ellicottae* is perforate, though to a lesser degree than the nasals (see Fig. 6 C). If the rhinarium extended across the roof of the rostrum and onto the lateral surface, this would highly diminish any space for masseter attachment. A stepwise reduction of the rostral origin of the superficial masseter (i.e., the masseteric tubercle) in the evolutionary lineage of euhapsines leading to *Paraeuhapsis* supports this notion (see Fig. 2). The development of the lip-closing musculature along the well-developed lateral rostral fossa may also have played a role in eliminating the masseter from the rostrum. The retreat of the masseter to the zygoma alone may also enhance the lateral motion of chewing utilized during the mastication of grasses, roots, and other geophytes. Shortening of the rostrum is yet another explanation that has been posited for secondary protrogomorphy in bathyergoids (Cox and Faulkes, 2014).

CONCLUSIONS

The osteology of the nasal bones in the Miocene *Paraeuhapsis ellicottae* is consistent with known features in modern taxa for the attachment of horns and we suspect it likely possessed a keratin fiber horn. The texture of the nasal bones must, at a minimum, be interpreted as the osteological signature of a dramatically thickened rhinarium. By comparison to other modern subterranean rodents and other members of the Euhapsini, *P. ellicottae* had the most rugose texture and an annular arrangement of Sharpey's fibers, indicating that the nasal boss likely served as the attachment site of the horn. Other euhapsines (e.g., *Euhapsis martini*) likely possessed rhinaria similar to the ones seen in living spalacines.

Secondary protrogomorphy likely results from a need to enhance the bite force necessary for burrowing behaviors. The elimination of the rostral attachment of the masseter as well as the increased temporalis musculature in the skull of *Paraeuhapsis* indicates that it was capable of producing a more powerful dorso–ventral bite force compared to the antero–posterior bite force, which is most likely a function of the need to strengthen the bite at the incisors during tooth-digging behavior.

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CONCLUSIONS

This dissertation is a revision of the taxonomy of the castorid tribe Euhapsini and a reinterpretation of the burrowing behaviors of the members of that group by comparison to modern and fossil subterranean rodents. A new species (*Euhapsis martini*) and a new genus (*Paraeuhapsis*) were described in Chapter 2, and the reassessment of the diversity of form in euhapsines allowed for additional questions to be asked about the functional anatomy of this group and other burrowing groups. Skull morphology, and the incisors in particular, is adapted in subterranean rodents to improve burrowing performance. Grooves on the upper incisors of burrowing rodents were found to have a strict correlation with diet in Chapter 3, as groove-toothed rodents never used chisel-tooth-digging behavior and tended to prefer grass to other food items. The incisor morphology—procumbency, wear-facet morphology, wear pattern at the tip, and grooved incisor enamel—of modern rodents was found herein to correlate with burrowing behavior, and, therefore, can be used in fossil taxa to interpret burrowing behavior in extinct organisms, as was shown in Chapter 4. Chapter 5 was an examination of the unique nasal structure of the new euhapsines *E. martini* and *Paraeuhapsis*, and they were shown to have unique keratinous nasal structures not seen in any living subterranean rodent.

The subfamily Palaeocastorinae had a diverse history which included members adapted for every known type of burrowing behavior. Most palaeocastorines (e.g., *Palaeocastor fossor*) were adapted for chisel-tooth digging, resulting in the deep (> 1.5 m below the surface) open burrow *Daimonelix*. The euhapsines were instead adapted for head-lift digging, and most likely restricted their burrowing activities to the upper portions (0.5–1.5 m deep) of the soil profile where the roots and geophytes were available, as was certainly the case for *Paraeuhapsis ellicottae* (Fig. 1). The skeletal evidence described in this dissertation for this behavior in

Figure 1—Life reconstruction of *Paraeuhapsis ellicottae* burrowing in the root zone < 0.5 m below the surface.

Paraeuhapsis includes: the greatly widened overall skull proportion; the dramatically broadened and tilted occiput; the formation of a secondary glenoid posterior to the mandibular fossa; the flat

and elongate upper incisor wear facets; the moderate upper incisor procumbency; and, in the case of the *P. ellicottae*, nasal bones with an annular region of dramatically increased rugosity surrounding a boss that most likely supported a keratin fiber horn. The observations consolidated in this dissertation have qualified Martin's (1987) statement that the skull of *Paraeuhapsis* makes it "one of the most highly derived fossorial rodents known".

The newly described *Euhapsis martini* was clearly an advanced subterranean rodent, but was still more primitive than any of the other known *Euhapsis*. Its close alignment with both *E. platyceps* and *E. luskensis* and its only superficial similarity to *Paraeuhapsis* is a clear indication of diversity in form and behavior in this group and was the justification for the formation of a new taxon for the specimens referable to *Paraeuhapsis*. The description of *E. martini* required some questions to be asked about the morphology of *P. ellicottae* and *P. breugerorum*: what was the function of the groove in the incisor, why did they have such unique cranial muscle attachments, what was the purpose of the secondary genoid, and what was the anatomy associated with the modified nasal bones? *Paraeuhapsis* has been shown to be a unique taxon that used these features to become even further specialized as a burrower. The groove in its incisors was an adaptation for shredding grass. The rearrangement of its cranial musculature in concert with its secondary glenoid allowed it to deliver a powerful bite at the incisors during head-lift digging. The modified nasals more than likely served as the attachment site for a horn in *P. ellicottae.*

Paraeuhapsis and *Euhapsis* have distinct cranial morphologies indicating that, though they were both head-lift diggers, they lived in slightly different environments and may have had subtly different behavior. There is strong environmental correlation between subterranean rodents and their environment, because they are adapted to eating specific food types and to

burrowing in particular soil types. Similarity in burrowing behavior to modern ctenomyids and batherygoids suggests that such beavers as *Palaeocastor* preferred seasonal environments. The head-lifting euhapsines instead preferred the most cool and dry times exemplified by C cycles, with *Euhapsis* preferring the transitional period and *Paraeuhapsis* preferring the terminal portion of Martin and Meehan's (2005) C cycle. Ongoing work should focus on finely discriminating environmental preferences in living subterranean rodents as a means of enhancing paleoenvironmental and paleopedological interpretations.

Subterranean rodents experience intense selection pressures, and are, therefore, broadly convergent in form (Nevo, 1999). The reduction of the eyes and ears, increased upper incisor procumbency, and development of a fusiform body are a few of only many adaptations seen in all subterranean rodents. Differences among subterranean rodents can be seen in the various modifications to the upper incisors: the degree of their procumbency; the change in the relative size of the incisors; and the differences in the morphology of the incisor wear facet. While these factors were used to help to interpret different burrowing behaviors in fossil rodents, ongoing research should attempt to relate more subtle differences in morphology and behavior to soil types and specific environmental parameters in order to deduce more specific ancient environments from the fossil record.

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Appendix I. Phylogenetic Analysis

PHYLOGENETIC METHODS

Wahlert's (1978) phylogeny relied primarily on the position of cranial foramina to determine relationships, and was the first modern attempt to interpret castorid relationships, though he was unconcerned with the relationships of palaeocastorines as they had not yet been united as such. Many of the characters from his phylogeny became the basis for later work. Martin (1987) named several euhapsine genera, so his work was the first attempt to interpret the evolutionary relationships within the group. Most later workers recovered results consistent with this scheme. The notable exception was Xu (1995, 1996) which recovered a paraphyletic Euhapsini, with *Euhapsis* + *Capatanka* forming a clade sister to *Fossorcastor* + *Nannasfiber* (now synononymized with *Pseudopalaeocastor*) based primarily on the morphology of the lower jaws. Korth's (2001) review demonstrated those jaw morphologies to be widely convergent, and reverted back to Martin's (1987) scheme with no revisions. The most comprehensive palaeocastorine phylogeny to date (Rybczynski, 2007) did not consider many euhapsine taxa, and did not consider any *Euhapsis sensu stricto* due to the reassignment herein of *E. ellicottae* and *E. breugerorum* to the new genus *Paraeuhapsis*.

The character matrix of Rybczynski (2007) was modified. Twelve taxa were included in the analysis; only a single representative member of the castorine lineage (*Steneofiber eseri*) was included to demonstrate its uniqueness from the derived palaeocastorines. Only characters pertinent to the skull and mandible were utilized (66 of the original characters utilized by Rybczynski, 2007). Fourteen new characters were added to this matrix, and several characters were modified or re-coded. Character codings were based on original character codings in

Rybczysnki (2007), but new and updated characters (and characters coded for taxa not previously considered) were coded based on material listed in following section. New and modified characters are noted in the character descriptions. Phylogenetic analysis was performed using TNT (Golobdoff et al., 2008) using traditional search algorithms. *Eutypomys thomsoni* was designated as the outgroup taxon. A single most parsimonious tree was found. Synapomorphic characters are reported for notable clades using the "list synapomorphies" command.

INVESTIGATED MATERIAL

1) *Agnotocastor coloradensis* - based on assorted material in the KUVP collections.
2) *Euhapsis luskensis* - F:AM
3) *Euhapsis martini* - AMNH 10818
4) *Euhapsis platyceps* - CM 1220
5) *Eutypomys thomsoni* - new characters coded based on available images and cast material in the KUVP collections
6) *Fossorcastor brachyceps* - cast of AMNH 12902
7) *Fossorcastor greeni* - KUVP 80845
8) *Palaeocastor* cf. *nebrascensis* - F:AM 64221, F:AM 64225
9) *Paraeuhapsis breugerorum* - KUVP 28376
10) *Paraeuhapsis ellicottae* - KUVP 48015, 48016
11) *Steneofiber eseri* - new characters coded based on available images
12) Unnamed euhapsine taxa. KUVP 125061. Considered by Rybczysnki (2007).

CHARACTER DEFINITIONS

Upper teeth are denoted by upper-case letters; lower teeth are denoted by lower-case letters. Upper and lower premolars are designated “P” and “p” respectively, whereas upper and lower molars are designated “M” and “m” respectively. Tooth positions are numbered from front to back. For example, “M1” is the first upper molar. Specialized dental nomenclature from Stirton (1935). Nomenclature for cranial foramina follows Wahlert (1974).

1. Ratio of skull width to length: (0) skull length exceeds bizygomatic width, (1) skull length equal or near equal to bizygomatic width. New character.
2. Pit on the lateral surface of the rostrum: (0) absent, (1) shallow), (2) deep. New character.
3. Rostrum cross-sectional shape, height/width: (0) < 1; (1) 1–1.15; (2) ≥ 1.15. Rostral dimensions are measured at anterior limit of premaxillary-maxillary suture. Character 2 of Rybczynski (2007).
4. Anterior edge of nasal relative to that of premaxilla: (0) anterior; (1) level; (2) posterior. Skull is viewed in lateral view and is oriented so that the cheek-tooth rows are horizontal. Character 3 of Rybczynski (2007).
5. Width of nasals divided by width of rostrum: (0) < 0.6; (1) ≥ 0.6. Rostral width taken at the dorsal limit of the incisor, within the maxilla. The dorsal limit of the incisor can be readily identified because the lateral surface of the maxillary bone bulges where it overlies the incisor. The nasal width measurement is taken at the same position along the rostrum. Character 4 of Rybczynski (2007).
6. Lateral margin of nasals in dorsal view: (0) nearly straight or only slightly convex; (1) posteriorly, margin is straight or slightly concave, and anteriorly it is convex; (2)

posteriorly, margin is straight and angled relative to midline, anterior margin is straight and parallel to midline; (3) strongly convex. Character 5 of Rybczynski (2007).

7. Nasal boss along midline suture: (0) absent, (1) present. New character.
8. Nasal height: (0) level with cranium height in lateral view, (1) greater than cranium height in lateral view. New character.
9. Ratio of rostrum length to skull length: (0) > 0.38, (1) ≤ 0.38. New character.
10. Position of posterior limit of premaxilla-maxilla suture in relation to posterior limit of incisive foramina: (0) posterior or level; (1) anterior. Character modified from Martin (1987). Character 6 of Rybczynski (2007).
11. Length of incisive foramina divided by diastema length: (0) > 0.24; (1) 0.15–0.24; (2) ≤ 0.15. Diastema length is the parasagittal distance from the anterior margin of the cheek tooth alveolus to the posterior margin of the incisal alveolus. Character modified from Korth (2002). Character 7 of Rybczynski (2007).
12. Posterior half of incisive foramen. Vertical position of lateral border of foramen in relation to midline ridge: (0) ventral; (1) level; (2) dorsal. Character modified from Martin (1987). Character 8 of Rybczynski (2007).
13. Muscle scar indicating presence of antorbital portion of deep masseter: (0) absent; (1) present, depression not pronounced; (2) present, depression confined to maxilla, anterior limit of muscle scar might be marked by a low, rounded ridge; (3) Present, depression largely located in maxilla, but also formed in the premaxilla. Anterior limit of depression marked by a sharp ridge. Character 9 of Rybczynski (2007).
14. Anterior margin of infraorbital foramen in lateral view: (0) concave; (1) straight and perpendicular to toothrow; (2) angled so foramen opens somewhat dorsally; (3) angled so

foramen opens somewhat ventrally; (4) obscured due to near elimination of opening (as in *Paraeuhapsis*). Modified from character 10 of Rybczynski (2007).

15. Origin of anterior superficial masseter: (0) zygomatic only, (1) upper half of rostrum, (2) ventrally below the infraorbital foramen (as in *Fossorcastor*), (3) attached to masseteric tubercle immediately ventral to anterior limit of zygoma (as in *Euhapsis*). This character is known to be primitive for rodents, but the character state of the outgroup taxon *Eutypomys* is 1. Modified from character 11 of Rybczynski (2007).
16. Anterolateral border of orbit: (0) formed by jugal with small jugal-lacrimal contact and large maxilla-lacrimal contact; (1) formed by jugal with large jugal-lacrimal contact and small, or absent, maxilla-lacrimal contact; (2) formed mostly by jugal with no jugal-lacrimal contact; (3) formed mostly by maxilla; (4) formed equally by maxilla and jugal; (5) jugal-maxilla suture appear to be fused dorsally. Character 12 of Rybczynski (2007).
17. Shape of foramen formed in choanal roof between presphenoid and palatine: (0) oval; (1); thin slit; (2) absent. Character 13 of Rybczynski (2007).
18. Anterolateral eminence on bulla: (0) absent; (1) present. In lateral view, the anterior eminence occurs at the anterolateral edge of the bulla. Character 14 of Rybczynski (2007).
19. Jugal thickness divided by jugal height: (0) ≥ 0.31; (1) < 0.31. Jugal height is a maximum, measured perpendicular to tooth row, in the plane of the lateral surface of the zygoma. Jugal thickness (mediolateral) is measured at the ventral margin of the zygomatic arch, immediately posterior to the jugal-maxilla contact. Character 15 of Rybczynski (2007).

20. Eminence of jugal: (0) more lateral than occiput, (1) even with occiput, (20) occiput more lateral than eminence (2). New character.
21. Ventral zygomatic margin: (0) concave, (1) convex. New character.
22. Zygomatic height at caudal end of orbit: (0) about equal to height of jugal-squamosal juncture, (1) about twice the height of jugal-squamosal juncture, (2) three or more times the height of the jugal-squamosal juncture. New character.
23. Zygomatic height when viewed laterally with tooth row horizontal: (0) height of zygoma below dorsal limit of cranium or rostrum; (1) height of zygoma even with dorsal limit of cranium or rostrum. New character.
24. Maxilla in palatal view, medial to cheek teeth: (0) flat, or slight midline ridge; (1) surface recessed, weak or rounded midline ridge; (2) surface recessed, prominent midline ridge; (3) deep, slit-like, lateral groove and rounded midline ridge. Character 16 of Rybczynski (2007).
25. Maxilla in palatal view, anterior to cheek teeth:(0) roughly flat with lateral, parasagittally oriented ridge; (1) with midline ridge and lateral ridge (lateral ridge usually weak); (2) with midline groove, possibly a slight midline ridge formed within the groove. Character 17 of Rybczynski (2007).
26. Maxilla-alisphenoid contact: (0) absent; (1) anterior limit located posterior to M3; (2) anterior limit located dorsal to M3; (3) anterior limit located dorsal, or dorsal and anterior to, M2-M3 junction. Character 18 of Rybczynski (2007).
27. Posterior maxillary foramen/notch shape: (0) notch; (1) enclosed lenticular foramen; (2) enclosed round foramen. Character 19 of Rybczynski (2007).

28. Posterior maxillary foramen/notch border composition: (0) between maxilla and palatine; (1) formed mostly within palatine; (2) formed entirely within palatine. Character 20 of Rybczynski (2007).
29. Ventral surface of palatine: (0) flat, or slightly recessed, possibly with a rounded midline ridge; (1) deeply recessed with a sharp midline ridge; (2) lateral, parasagittal, slit-like groove. Character 21 of Rybczynski (2007).
30. Horizontal location of palatine's posterior margin: (0) posterior to M3; (1) level with posterior margin of M3; (2) level with M3; (3) level with M2/M3 junction. Character 22 of Rybczynski (2007).
31. Location of posterior palatine foramen: (0) palatine bone; (1) palatine-maxilla suture. Character 23 of Rybczynski (2007).
32. Location of sphenopalatine foramen: (0) between orbital process of maxilla and orbital process of palatine; (1) within maxilla. Character 24 of Rybczynski (2007).
33. Location of ethmoid foramen: (0) frontal; (1) frontal-orbitosphenoid suture. Character 25 of Rybczynski (2007).
34. Location of dorsal palatine foramen: (0) palatine; (1) maxilla-palatine suture; (2) maxilla-orbitosphenoid suture; (3) maxilla; (4) maxilla-alisphenoid suture; (5) absent. Character 26 of Rybczynski (2007).
35. Interorbital foramen(ina) posterior to optic foramen: (0) absent; (1) present. Character 27 of Rybczynski (2007).
36. Sphenofrontal foramen: (0) present; (1) absent. Character 28 of Rybczynski (2007).

37. Shape of anterior margin sphenoidal fissure in lateral view: (0) anterior margin is concave; (1) anterior margin is nearly straight, and is roughly vertical or slopes so that the fissure opens dorsally. Character 29 of Rybczynski (2007).
38. Masticatory and buccinator foramina: (0) separate; (1) conjoint. Character 30 of Rybczynski (2007).
39. Foramen ovale accesorius: (0) present, forming a closed foramen; (1) present, but foramen not fully enclosed; (2) absent. Character 31 of Rybczynski (2007).
40. Middle lacerate foramen: (0) absent, or obscured by bulla; (1) present and separate from foramen ovale; (2) present and confluent with foramen ovale. Character 32 of Rybczynski (2007).
41. Posterior alar fissure: (0) absent, large alisphenoid-bulla contact present; (1) present, and forming a closed foramen; (2) present, and fissure open ventrally. Character 33 of Rybczynski (2007).
42. Sculpting (rugosities) on dorsal surface of parietals: (0) absent; (1) present. Character 34 of Rybczynski (2007).
43. Interparietal: (0) present; (1) absent or fused. Character 35 of Rybczynski (2007).
44. Sagittal crest(s): (0) single, or closely opposed; (1) double for length of braincase; (2) double in parietals, but single in interparietal region (= lyrate shaped). Character 36 of Rybczynski (2007).
45. Height of sagittal crest: (0) prominent, (1) indistinct from parietals. New character.
46. Ventral projection of squamosal separating external auditory meatus from mastoid: (0) absent; (1) present. Character 37 of Rybczynski (2007).

47. Mandibular glenoid (squamosal) extent: (0) medial but not posterior to jugal; (1) medial and posterior to jugal with lateral margin of posterior region angled posteriorly toward midline; (2) medial and posterior to jugal with lateral margin of posterior region angled parallel to midline and not completely covered by occiput (unique character of *Euhapsis luskensis*); (3) medial and posterior to jugal with lateral margin of posterior region angled parallel to midline and completely covered by occiput. Modified from character 38 of Rybczynski (2007).
48. Temporal foramen(ina): (0) single; (1) multiple. Character 39 of Rybczynski (2007).
49. Auditory tube: (0) absent; (1) present. Character 40 of Rybczynski (2007).
50. Auditory bulla in ventral view with medial process: (0) absent or forming only a very small bump; (1) present, forming a rugose flange that projects anteriorly; (2) present, forming a rugose flange that projects antero-ventrally. Character 41 of Rybczynski (2007).
51. Evidence for the presence of a stapedial artery: (0) present; (1) absent. Character 42 of Rybczynski (2007).
52. Basioccipital ventral surface: (0) with a midline ridge; (1) deep, sub-rectangular recess occupying entire space between bulla, flat dorsally; (2) deeply recessed anteriorly, midline bump located posteriorly. Character 43 of Rybczynski (2007).
53. Angle of occiput: (0) approximately perpendicular or sloping anteriorly up to 10°; (1) sloping anteriorly up to 10°–20°; (2) sloping anteriorly more than 20°; (3) lower portion perpendicular, upper portion sloping more than 20°, unique character of *Euhapsis luskensis*. Character modified from (Martin, 1987). Skull viewed in lateral view with

cheek teeth horizontal. Condyles were not considered in determination of occiput slope. Modified from character 44 of Rybczynski (2007).

54. "Squamoso-mastoid" foramen: (0) absent; (1) present. The "squamoso-mastoid" foramen is a small foramen, visible in occipital view, and is located at the lateral margin of the mastoid. Character 45 of Rybczynski (2007).
55. Upper incisor shape. Anterior surface of incisor; blade edge in anterior view: (0) convex; convex; (1) convex; straight; (2) flat; straight. Character 46 of Rybczynski (2007).
56. Upper incisor cross-sectional shape. Incisor width divided by length: (0) ≤ 0.8; (1) 0.8–1; (2) ≥ 1. Character 47 of Rybczynski (2007).
57. Upper incisor enamel: (0) smooth; (1) grooved; (2) faintly grooved or rugose. Character 48 of Rybczynski (2007).
58. Upper incisor procumbency, procumbency measured as in van der Merwe and Botha (1998): (0) < 110°, (1) 110°–115°, (2) > 115°. New character.
59. Angle of upper incisor wear facet: (0) 155°–160°; (1) < 155°; (2) > 160°. New character.
60. Morphology of upper incisor wear facet: (0) elongate and shallowly curved; (1) short and highly curved; (2) flat and elongate. New character.
61. Upper third premolar: (0) present; (1) absent. Character 49 of Rybczynski (2007).
62. Distance between tooth rows anteriorly divided by the distance between tooth rows posteriorly: (0) ≥ 0.92; (1) 0.92–0.7; (2) ≤ 0.7. Distance between toothrows anteriorly measured at midpoint of the anterior rim of the left and right P4 alveoli. Distance between toothrows posteriorly measured at midpoint of the posterior rim of M3 alveoli. Character 50 of Rybczynski (2007).

63. M1 in occlusal view: (0) width > length; (1) width ≤ length. Character 1 of Rybczynski (2007).
64. Comparison of M2 and M3, mesiodistal (= anteroposterior) dimensions: (0) M2 ≥ M3; (1) M2 < M3. Measurement taken along occlusal surface of the tooth. Only adult specimens are considered. Character 51 of Rybczynski (2007).
65. Molar shape: (0) brachydont, with distinct, convex-sided crowns, multiple roots visible near alveolar rim; (1) No flexus/id, multiple fossettes on occlusal surface; (2) hypoflexus/id present, multiple fossettes on occlusal surface, mesoflexus/id may be present but is not persistent (i.e., stria/id associated with mesoflexus/id is very short). Modified from character 52 of Rybczynski (2007).
66. J.14 - Distance between the posterior end of tooth row and anterior limit of auditory bullae: (0) distance ≥ length of bullae, (1) less than length but greater than half the length of the bullae, (2) less than half the length of the bullae. New character.
67. Lower incisor shape. Anterior surface of incisor; blade edge in anterior view: (0) convex; convex; (1) semi-flat; convex, (2) semi-flat; straight; (3) flat; straight. Character modified from (Stirton, 1935). “Semi-flat” lower incisors are flat near the medial edge of tooth but curved toward lateral edge. Character 53 of Rybczynski (2007).
68. Lower incisor cross-sectional shape. Incisor width divided by length: (0) ≤ 0.7; (1) 0.7–1; (2) ≥ 1. Character 54 of Rybczynski (2007).
69. Lower incisor interstitial wear facet: (0) present; (1) absent. Interstitial wear near the apex of the incisor indicates symphyseal mobility. Character 55 of Rybczynski (2007).

70. In lateral view, vertical position relative to tooth row of mandibular diastema; of posterior rim of lower incisor alveolus: (0) level; level or above; (1) below; level or above (2) below; below. Character 56 of Rybczynski (2007).
71. Digastric process in lateral view: (0) absent; (1) small, barely visible in lateral view; (2) or well developed. Character 57 of Rybczynski (2007).
72. Horizontal position of digastric process relative to anterior margin of p4: (0) Anterior; (1) Level; (2) Posterior. Mandible viewed in lateral view with tooth row oriented horizontally. Character 58 of Rybczynski (2007).
73. Fossa located near anterior limit of pterygoid fossa: (0) absent, or slight; (1) present and well-defined. Character 59 of Rybczynski (2007).
74. Ascending ramus of mandible in lateral view obscures: (0) part of m3; (1) m3 and up to half of m2; (2) m3 and more than half of m2, but not m1; (3) m3, m2 and part or all of m1. Character 60 of Rybczynski (2007).
75. Line drawn from posterior tip of coronoid to posterior tip of angle, in posterior view: (0) located just medial to, but contacting or, nearly intersecting condyle; (1) located at least half of the condyle-width lateral to medial edge of condyle. Character 61 of Rybczynski (2007).
76. Mandibular condyle width divided by length: (0) ≤ 0.61; (1) 0.61–0.75; (2) ≥ 0.75. Character 62 of Rybczynski (2007).
77. Capsular process: (0) absent; (1) present. Modified from character 63 of Rybczynski (2007).

78. Location of base of capsular process relative to condyle: (0) below and anterior; (1) below; (2) below and posterior. Mandible viewed in lateral view with tooth row oriented horizontally. Character 64 of Rybczynski (2007).
79. Shape of mandibular angle in lateral view: (0) rounded; (1) pointed. If anterodorsal point of angle forms an angle of over 90°, it is considered rounded. Character 65 of Rybczynski (2007).
80. Location of mandibular angle dorsal-margin relative to toothrow: (0) below; (1) approximately level; (2) above. Character 66 of Rybczynski (2007).

CHARACTER MATRIX

Agnotocastor coloradensis

002?1 0000[1,2] 0?2?1 ????0 000?1 11?02 ????? ????? ???00 ?0??? ????1 10000 0?021 001[0,1]1 2001? 00??0

Euhapsis luskensis

?20?1 ??011 002?3 ??0?2 ???[0,1]2 22102 1???0 ?1??? ?11?1 02010 ?0302 20122 10102 13101 22?30 21002

Euhapsis martini

11001 20010 00213 ??001 01112 1??23 ????? ????? [0,1]1120 10010 ?0002 20??2 10002 1?1?1 22?20 2?002

Euhapsis platyceps

120?1 2?01? 00213 0?002 12112 ???2? ?10?0 ?1?0? 11111 03010 ?0202 20122 1??02
??1?1 ???3? ?????

Eutypomys thomsoni

00000 00000 01101 ?10?0 00000 12102 011[2,3]1 00000 ?1000 00000 00000 00000
00001 0000[0,2] 100[0,1]? ?00?0

Fossorcastor brachyceps

?21?1 ??010 10222 0?000 12?12 20[1,2]22 ????? ????? ?1101 01010 ?0102 ?0??1
10002 13211 22?30 2100?

Fossorcastor greeni

0?1?1 ??01? ??222 ?20?0 ???3? 21?22 1???? ????? 11?0? ?1?10 101?2 20111 11002
1311? ?003? ???0?

Palaeocastor cf. *nebrascensis*

00111 ?0001 02[1,2]?1 41000 ??012 12103 11?3? ?10?? 010[0,1]? 10010
000[0,1]2 10000 11002 ????[1,2] [1,2]101? ?000?

Paraeuhapsis breugerorum

?2221 ?1111 00240 ?[1,2]012 ???12 2[0,1]022 0???0 ?100? ?1101 03010 10102
11212 100?2 13111 21031 21002

Paraeuhapsis ellicotae

?2221 21111 10240 [0,2][1,2]0?2 ???12 32022 ?10[2,3]0 ?100? 11101 03010 10202
21??2 10002 2???? ????? ?????

Steneofiber eseri

002?1 [0,1]0000 0[1,2]231 [0,2,5]0000 000?1 1[0,1]10[1,2] [0,1]103[0,1]
0[0,1][0,1]0? ?[0,1]111 [1,2][0,1]0[1,2]0 10000

Unnamed euhapsine taxon

01111 10010 00221 ??0?? ??012 3[1,2]?02 ????? ????? ????? ?[1,2]?10 ??1?2
10211 11002 231?1 20031 100?2

SYNAPOMORPHIES

Tree 0 :

Eutypomys thomsoni:

No autapomorphies

Agnotocastor coloradensis:

Char. 9: 0 --> 12

Char. 63: 0 --> 2

Steneofiber eseri:

Char. 16: 1 --> 0

Char. 43: 0 --> 2

Char. 47: 0 --> 1

Char. 49: 0 --> 1

Char. 51: 0 --> 2

Char. 53: 0 --> 1

Unnamed taxon:

Char. 74: 0 --> 1

Palaeocastor cf. *nebrascensis*:

Char. 9: 0 --> 1

Char. 15: 0 --> 4

Char. 29: 2 --> 3

Char. 71: 0 --> 1

Euhapsis martini:

Char. 21: 2 --> 1

Char. 25: 2 --> 1

Char. 29: 2 --> 3

Char. 43: 0 --> 2

Char. 44: 1 --> 0

Char. 73: 3 --> 2

Euhapsis platyceps:

No autapomorphies

Euhapsis luskensis:

Char. 28: 2 --> 0

Char. 46: 3 --> 2

Fossorcastor brachyceps:

Char. 10: 0 --> 1

Char. 67: 1 --> 2

Fossorcastor greeni:

Char. 23: 1 --> 3

Paraeuhapsis breugerorum:

Char. 55: 2 --> 1

Paraeuhapsis ellicotae:

Char. 10: 0 --> 1

Char. 25: 2 --> 3

Char. 65: 1 --> 2

Node 13:

No synapomorphies

Node 14:

Char. 44: 0 --> 1

Char. 60: 0 --> 1

Char. 64: 1 --> 2

Node 15:

Char. 8: 0 --> 1

Char. 46: 0 --> 1

Char. 52: 0 --> 1

Char. 58: 0 --> 1

Char. 59: 0 --> 1

Char. 73: 1 --> 3

Node 16:

Char. 2: 2 --> 1

Char. 24: 1 --> 2

Char. 54: 1 --> 2

Node 17:

Char. 2: 1 --> 0

Char. 13: 2 --> 1

Char. 14: 2 --> 3

Char. 59: 1 --> 2

Node 18:

Char. 61: 1 --> 0

Char. 71: 0 --> 2

Node 19:

Char. 14: 1 --> 2

Char. 28: 0 --> 2

Char. 55: 1 --> 2

Node 20:

Char. 58: 1 --> 2

Node 21:

Char. 9: 0 --> 1

Node 22:

Char. 2: 0 --> 2

Char. 7: 0 --> 1

Char. 13: 1 --> 4

Char. 14: 3 --> 0

Char. 27: 1 --> 0

Char. 56: 0 --> 1

Appendix II. Upper Incisor Groove Patterns of Modern Rodents

Genus	Family	Groove Pattern	Reference
Bathyergus	Bathyergidae	Single deep groove	personal observation
Hydrochoerus	Caviidae	Single groove	personal observation
Auliscomys	Cricetidae	not reported	Ohazama et al. (2010)
Euneomys	Cricetidae	not reported	Ohazama et al. (2010)
Irenomys	Cricetidae	not reported	Ohazama et al. (2010)
Neotomys	Cricetidae	narrow groove in outer corner	Nowak (1999)
Phyllotis	Cricetidae	not reported	Ohazama et al. (2010)
Reithrodon	Cricetidae	deep median groove	Nowak (1999)
Reithrodontomys	Cricetidae	grooved upper incisors	Nowak (1999)
Synaptomys	Cricetidae	shallow groove at outer edge	Nowak (1999)
Ctenodactylus	Ctenodactylidae	not reported	Ohazama et al. (2010)
Felovia	Ctenodactylidae	weakly grooved	Nowak (1999)
Massoutiera	Ctenodactylidae	not reported	Ohazama et al. (2010)
Dipus	Dipodidae	not reported	Ohazama et al. (2010)
Jaculus	Dipodidae	single groove	Osborn and Helmy (1980)
Stylodipus	Dipodidae	not reported	Ohazama et al. (2010)
Eozapus	Dipodidae	not reported	Ohazama et al. (2010)
Napaeozapus	Dipodidae	not reported	Ohazama et al. (2010)
Zapus	Dipodidae	grooved in front	Nowak (1999)
Cratogeomys	Geomyidae	single groove	Merriam (1895)
Geomys	Geomyidae	two grooves	Nowak (1999)
Orthogeomys	Geomyidae	single median groove located near edge of tooth, but a lingual groove is sometimes also present	Nowak (1999)
Pappogeomys	Geomyidae	single groove	Merriam (1895)
Zygogeomys	Geomyidae	two grooves	Nowak (1999)
Chaetodipus	Heteromyidae	not reported	Ohazama et al. (2010)
Dipodomys	Heteromyidae	single medial groove	personal observation
Microdipodops	Heteromyidae	not reported	Ohazama et al. (2010)
Perognathus	Heteromyidae	not reported	Ohazama et al. (2010)
Ammodillus	Muridae	not reported	Ohazama et al. (2010)
Crateromys	Muridae	not reported	Ohazama et al. (2010)
Deomys	Muridae	2 minute grooves	Nowak (1999)
Desmodilliscus	Muridae	not reported	Ohazama et al. (2010)
Desmodillus	Muridae	not reported	Ohazama et al. (2010)
Desmomys	Muridae	not reported	Ohazama et al. (2010)
Dipodillus	Muridae	single groove	Osborn and Helmy (1980)

Gerbilliscus	Muridae	two shallow grooves	Nowak (1999)
Gerbillurus	Muridae	not reported	Ohazama et al. (2010)
Gerbillus	Muridae	grooved (sometimes indistinctly)	Nowak (1999)
Golunda	Muridae	not reported	Ohazama et al. (2010)
Leimacomys	Muridae	weakly grooved	Nowak (1999)
Meriones	Muridae	narrow groove	Nowak (1999)
Microdillus	Muridae	not reported	Ohazama et al. (2010)
Microhydromys	Muridae	not reported	Ohazama et al. (2010)
Mylomys	Muridae	single groove	Nowak (1999)
Otomys	Muridae	at least one groove in each upper and lower incisor	Nowak (1999)
Pachyuromys	Muridae	slightly grooved	Nowak (1999)
Pelomys	Muridae	not reported	Ohazama et al. (2010)
Rhombomys	Muridae	2 grooves	Nowak (1999)
Sekeetamys	Muridae	single groove	Osborn and Helmy (1980)
Tatera	Muridae	single groove	Nowak (1999)
Taterillus	Muridae	single groove	Nowak (1999)
Vandeleuria	Muridae	not reported	Ohazama et al. (2010)
Prometheomys	Muridae: Arvicolinae	single (light) groove	Nowak (1999)
Dendromus	Nesomyidae	single groove	Denys and Aniskine (2012)
Dendroprionomys	Nesomyidae	single groove	Kingdon et al. (2013)
Malacothrix	Nesomyidae	not reported	Ohazama et al. (2010)
Steatomys	Nesomyidae	upper teeth are grooved	Nowak (1999)
Aeretes	Sciuridae	single groove	Nowak (1999)
Rheithrosciurus	Sciuridae	7 to 10 minute grooves	Nowak (1999)
Thryonomys	Thryonomyidae	3 deep grooves	Nowak (1999)

Appendix III. Burrowing and Diet of Grooved Rodents

Genus	Family	Subterranean?	Burrowing Style	Reference	Diet	Reference
Bathyergus	Bathyergidae	yes	Scratch	van der Merwe and Botha (1998); Bennett et al. (2009)	entire portions of plants, grasses, bulbs, tubers	Bennett and Jarvis (1995); Herbst and Bennett (2006)
Hydrochoerus	Caviidae	no	n/a	n/a	grasses and reeds	Mones and Ojasti (1986)
Auliscomys	Cricetidae	no	occaisonal burrowing	Nowak (1999)	unknown	n/a
Euneomys	Cricetidae	no	Variable preferences	Nowak (1999)	seeds, insects	Kelt (1994)
Irenomys	Cricetidae	no	not described	Kelt (1993)	seeds, fruit, green vegetation, fungi	Kelt (1993)
Neotomys	Cricetidae	no	n/a	Nowak (1999)	unknown	n/a
Phyllotis	Cricetidae	no	unknown	Kramer et al. (1999)	insects, forbs, fruit, seeds, fruit	Kramer et al. (1999)
Reithrodon	Cricetidae	no	digs vertical burrows and shares burrows with *Ctenomys*	Pardiñas and Galliari (2001)	grasses	Pardiñas and Galliari (2001)
Reithrodontomys	Cricetidae	no	occupies burrows of others	Davis (1974)	Seeds, shoots, occaisonal insects, green parts of plants	Davis (1974); Spencer and Cameron (1982); Nowak (1999)
Synaptomys	Cricetidae	no	some burrowing	Nowak (1999)	roots, green parts of low vegetation, invertebrates	Nowak (1999)
Ctenodactylus	Ctenodactylidae	no	n/a	Nowak (1999)	leaves, stalks, seeds, flowers	Nowak (1999)
Felovia	Ctenodactylidae	no	n/a	Nowak (1999)	leaves, stalks, seeds, flowers	Nowak (1999)
Massoutiera	Ctenodactylidae	no	n/a	Nowak (1999)	leaves, stalks, seeds, flowers	Nowak (1999)

Dipus	Dipodidae	no	rest in burrows by day	Kingdon et al. (2013)	all portions of vegetation	Nowak (1999)
Jaculus	Dipodidae	no	digs a burrow	Kingdon et al. (2013)	roots, sprouts, seeds, grains, cultivated vegetables	Nowak (1999)
Stylodipus	Dipodidae	no	rest in burrows by day	Kingdon et al. (2013)	lichens, rhizomes, bulbs, seeds, wheat	Nowak (1999)
Eozapus	Dipodidae	no	unknown	n/a	unknown	n/a
Napaeozapus	Dipodidae	no	digs a burrow	Whitaker and Wrigley (1972)	primarily seeds, but also fungi, insects, fruits, nuts, and other vegetation	Whitaker and Wrigley (1972)
Zapus	Dipodidae	no	Scratch	Whitaker (1972)	seeds preferably, but also fungus, nuts, berries, fruits, insects	Whitaker (1972)
Cratogeomys	Geomyidae	yes	Scratch Chisel-tooth	Lessa and Thaeler (1989)	rhizomes and roots of grasses	Hegdal et al. (1965)
Geomys	Geomyidae	yes	Scratch	Lessa and Thaeler (1989)	grasses, roots	Tilman (1983); Williams and Cameron (1986)
Orthogeomys	Geomyidae	yes	Scratch	Stein (2000)	wide variety of vegetable matter; crops	Nowak (1999)
Pappogeomys	Geomyidae	yes	Scratch	Stein (2000)	roots, stems, bark on tree roots, crops	Davis (1974)
Zygogeomys	Geomyidae	yes	Scratch	Stein (2000)	crops	Nowak (1999)
Chaetodipus	Heteromyidae	no	scratch	Nowak (1999)	seeds	Davis (1974)
Dipodomys	Heteromyidae	no	Scratch	Best (1988)	seeds and grasses; leaves of *Atriplex confertifolia*, and seeds; rarely arthropods and fungus	Schroder (1979) Hayssen (1991)

Microdipodops	Heteromyidae	no	simple, short, unbranched tunnels	O'Farrell and Blaustein (1974)	seeds and insects	O'Farrell and Blaustein (1974)
Perognathus	Heteromyidae	no	scratch	Nowak (1999)	seeds, green vegetation, insects	Nowak (1999)
Ammodillus	Muridae	no	digs in sandy soils	Kingdon et al. (2013)	unknown	n/a
Crateromys	Muridae	no	n/a	Nowak (1999)	bark and buds of pine trees, fruit	Nowak (1999)
Deomys	Muridae	no	n/a	Nowak (1999)	insects, small invertebrates, occaisional vegetable matter	Nowak (1999)
Desmodilliscus	Muridae	no	complex burrows	Nowak (1999)	seeds	Nowak (1999)
Desmodillus	Muridae	no	communal burrowing	Nel (1967)	seeds	Nel (1967)
Desmomys	Muridae	no	rarely, primarily arboreal	Nowak (1999)	grass, swamp vegetation	Nowak (1999)
Dipodillus	Muridae	no	scratch	Nowak (1999)	succulents and insects	Osborn and Helmy (1980)
Gerbilliscus	Muridae	no	digs in sandy soils	Kingdon et al. (2013)	seeds, plant material	Mulungu et al. (2011)
Gerbillurus	Muridae	no	simple, short, unbranched tunnels	Perrin et al. (1999)	seeds, insects, green vegetation	Perrin et al. (1999)
Gerbillus	Muridae	no	scratch	Agrawal (1967)	seeds, green plant matter	Degen et al. (1997)
Golunda	Muridae	no	rarely	Nowak (1999)	grasses	Nowak (1999); Rodrigues et al. (2008)
Leimacomys	Muridae	no	unknown	Nowak (1999)	unknown	Nowak (1999)
Meriones	Muridae	no	does burrow	Koffler (1972)	fruit, seeds, insects	Koffler (1972)
Microdillus	Muridae	no	does burrow	Nowak (1999)	unknown	n/a
Microhydromys	Muridae	no	n/a	Helgen et al. (2010)	invertebrates	Helgen et al. (2010)
Mylomys	Muridae	no	n/a	Nowak (1999)	grass stems and leaves	Nowak (1999)

Otomys	Muridae	no	some do	Nowak (1999)	grasses, semiaquatic plants, shoots, grains, seeds, berries, roots, bark	Nowak (1999)
Pachyuromys	Muridae	no	does burrow	Felt et al. (2008)	plant material, insects	Felt et al. (2008)
Pelomys	Muridae	no	n/a	Nowak (1999)	grasses, swamp vegetation (reeds), stems, leaves, and seeds	Nowak (1999); Rodrigues et al. (2008)
Rhombomys	Muridae	no	complex burrows	Nowak (1999)	desert plants	Nowak (1999)
Sekeetamys	Muridae	no	burrows below bolders and ledges	Nowak (1999)	seeds, succulent vegetation, insects	Osborn and Helmy (1980)
Tatera	Muridae	no	scratch	Agrawal (1967)	grass	Senzota (1984)
Taterillus	Muridae	no	do burrow	Nowak (1999)	seeds, insects	Nowak (1999)
Vandeleuria	Muridae	no	n/a	Agrawal (1967)	fruits, buds, shoots	Nowak (1999)
Prometheomys	Muridae: Arvicolinae	yes	Scratch	Gambaryan & Gasc (1993)	Roots, bulbs, and above ground plant portions	Gromov and Polyakov (1992)
Dendromus	Nesomyidae	no	scratch	Nowak (1999)	seeds, berries, insects, small lizards, bird eggs and nestlings	Nowak (1999)
Dendroprionomys	Nesomyidae	no	n/a	Kingdon et al. (2013)	insects	Nowak (1999)
Malacothrix	Nesomyidae	no	scratch	Nowak (1999)	green vegetable matter	Nowak (1999)
Steatomys	Nesomyidae	no	scratch	Nowak (1999)	seeds, grass bulbs, insects	Nowak (1999)
Aeretes	Sciuridae	no	n/a	Nowak (1999)	unknown	Jackson (2012)
Rheithrosciurus	Sciuridae	no	unknown	Nowak (1999)	fruits and seeds	Nowak (1999); Payne et al. (1985)
Thryonomys	Thryonomyidae	no	scratch	Nowak (1999)	grass, cane, bark, nuts, fruit, crops	Nowak (1999)

Appendix IV. Burowing and Diet of Grooveless Rodents

Genus	Family	Subterranean?	Burrowing Style	Reference	Diet	Reference
Cryptomys	Bathyergidae	yes	Chisel-tooth	Genelly (1965)	bulbs, tubers, roots	Genelly (1965)
Fukomys	Bathyergidae	yes	Chisel-tooth	Lovegrove (1989); Van Daele et al. (2009)	hard bulbs, tubers, roots	Jarvis et al. (1998); Kawalika and Burda (2007); Van Daele et al. (2009)
Georychus	Bathyergidae	yes	Chisel-tooth	Bennett et al. (2006)	Primarily geophytes, but ca. 6% of above ground structures	Bennett et al. (2006)
Heliophobius	Bathyergidae	yes	Chisel-tooth	Jarvis and Sale (1971)	underground plant organs	Šumbera et al. (2007)
Heterocephalus	Heterocephalidae	yes	Chisel-tooth	Jarvis and Sale (1971); Lovegrove (1989)	tubers, bulbs, corms	Busch et al. (2000)
Thomomys	Geomyidae	yes	Chisel-tooth	Lessa and Thaeler (1989)	preferably shoots of forbs, also shoots of grasses, roots during low plant productivity	Jenkins and Bollinger (1989); Verts and Carraway (1999); Reichman (2007)
Ellobius	Cricetidae	yes	Chisel-tooth Head-lift	Agrawal (1967); Gambaryan & Gasc (1993); Coskun (2001)	corms, bulbs, tubers, rossettes	Coşkun (2001)
Ctenomys	Octodontidae	yes	Scratch minor chisel-tooth	Camin et al. (1995); Vassallo (1998)	Grasses; roots avoided	Busch et al. (2000); Camin and Madoery (1994)
Octodon	Octodontidae	yes	Scratch Chisel-tooth	Ebensperger and Bozinovic (2000)	Grasses, leaves, seeds	Bozinovic et al. (2003)
Spalacopus	Octodontidae	yes	Chisel-tooth	Reig (1970)	tubers and bulbs	Torres-Mura and Contreras (1998); Begall and Gallardo (2000)

Tachyoryctes	Rhizomyinae	yes	Chisel-tooth	Jarvis and Sale (1971)	roots and shoots	Busch et al. (2000)
Cannomys	Spalacidae	yes	Chisel-tooth	Flynn (1990)	Bamboo roots; subterranean plant structures	Flynn (1990)
Eospalax	Spalacidae	yes	Scratch Head-lift	Zhang (2007)	preferably roots and rhizomes, but occaisionally shoots	Zhang (2007)
Myospalax	Spalacidae	yes	Scratch Head-lift	Gambaryan & Gasc (1993)	roots and grains	Nowak & Paradiso (1983)
Nannospalax	Spalacidae	yes	Head-lift	Nevo (1961); Heth (1989); Gambaryan & Gasc (1993); Zuri et al. (1999)	bulbs, corms, fleshy roots	Heth et al. (1989)
Rhizomys	Spalacidae	yes	Chisel-tooth	Flynn (1990)	Bamboo roots	Flynn (1990)
Spalax	Spalacidae	yes	Head-lift Chisel-tooth	Nevo (1961)	roots, bulbs, corms, tubers, and underground plant parts; occaisonal above ground feeding on grasses, seeds, superificial roots, and insects	Nevo (1961); Nowak & Paradiso (1983)
Cynomys	Sciuridae	no	Scratch	Hoogland (1995)	grasses	Slobodchikoff et al. (2009)
Aplodontia	Aplondontidae	no	Scratch	Carraway and Verts (1993)	bark, conifer needles, ferns, leaves	Arjo (2007)

Appendix V. References for Appendices II–IV

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Appendix VI. Upper Incisor Measurements of Fossil Rodents

Taxon	Specimen number	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Incisor groove?	Avg length/IB	Avg facet/avg eruption
Palaeocastor penninsulatus	AMNH 6998	119	3.75	4.11	n/a	n/a	3.75	4.08	6.79	5.01	149	10.65	no	0.3845	0.7378
Palaeocastor cf. *nebrascensis*	F:AM 64225	105	3.57	3.31	6.52	5.43	3.61	3.31	5.94	5.04	154	8.01	no	0.4132	0.8402
Unnamed euhapsine	KUVP 125061	117	3.97	3.81	n/a	n/a	3.89	3.8	8.11	7.02	139	10.22	no	0.3723	0.8655
Palaeocastor cf. *nebrascensis*	F;AM 64221	102	3.44	3.52	6.54	4.83	3.42	3.57	5.87	5.36	154	8.11	no	0.4371	0.8211
Palaeocastor sp.	CM 14231	123	4.03	3.52	3.22	4.7	4.03	3.46	3.13	4.65	132	9.22	no	0.3785	1.4724
Palaeocastor sp.	AMNH 12897	138	4.38	4.74	8.85	8.75	n/a	n/a	n/a	n/a	141	n/a	no	n/a	0.9887
Palaeocastor sp.	KUVP 28372	110	4.92	5.14	11.66	9.23	4.95	5.1	10.87	8.56	132	12.77	no	0.4009	0.7896
Palaeocastor sp.	KUVP 28380	114	5.55	5.54	9.97	9.67	5.49	5.59	9.82	9.61	155	12.83	no	0.4337	0.9742
Palaeocastor sp.	KUVP 28386	126	n/a	n/a	n/a	n/a	4.83	4.65	5.21	7.05	152	n/a	no	n/a	1.3531
Palaeocastor sp.	KUVP 155839	117	5.38	5.64	n/a	n/a	5.41	5.64	10.54	8.51	138	13.33	no	0.4231	0.8074
Palaeocastor sp.	KUVP 28385	130	n/a	n/a	n/a	n/a	4.52	4.95	10.74	6.38	141	n/a	no	n/a	0.5940
Palaeocastor fossor	KUVP 48019	122	n/a	n/a	n/a	n/a	4.81	4.95	10.84	7.69	127	n/a	no	n/a	0.7094
Pseudopalaeocastor barbouri	KUVP 48018	102	3.68	3.6	6.98	6.21	3.66	3.61	6.98	6.14	142	8.99	no	0.4010	0.8846
Fossorcastor greeni	KUVP 80845	116	3.78	3.65	7.02	6.67	3.77	3.68	7.17	6.6	150	9.26	no	0.3957	0.9351
Euhapsis martini	AMNH 10818	n/a	4.03	3.95	n/a	n/a	4.01	3.94	n/a	n/a	n/a	8.56	no	0.4608	1*

Taxon	Specimen number	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Incisor groove?	Avg length/IB	Avg facet/avg eruption
Euhapsis platyceps	CM 1220	110	4.2	3.77	6.83	7.18	3.96	3.77	6.8	7.62	164	9.33	no	0.4040	1.0858
Euhapsis luskensis	F:AM 64589	115	3.14	3.15	6.5	6.5	3.05	3.14	n/a	n/a	163	9.09	no	0.3459	1*
Paraeuhapsis breugerorum	KUVP 28376	121	4.04	4.19	7.65	8.09	4.02	4.19	6.48	8.32	150	9.66	yes	0.4337	1.1613
Paraeuhapsis ellicottae	KUVP 48015	n/a	4.32	4.01	n/a	n/a	4.29	3.98	n/a	n/a	n/a	9.88	yes	0.4043	n/a
Palaeocastor magnus	KUVP 28388	83	5.64	5.76	22.05	11.61	5.57	5.83	16.63	8.71	153	15.39	no	0.3765	0.5253
Palaeocastor fossor	KUVP 28383	111	4.56	4.35	9.88	7.38	4.51	4.32	9.54	6.96	158	10.38	no	0.4176	0.7384
Ceratogaulus minor	KUVP 6886	114	4.42	3.68	2.94	5.48	4.1	3.64	n/a	n/a	173	10.89	yes	0.3360	1.8639
Mylagaulus laevis	KUVP 9808	n/a	4.44	3.16	*	*	n/a	n/a	n/a	n/a	n/a	n/a	yes	n/a	1*

Appendix VII. Upper Incisor Measurements of Modern Rodents

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Avg length/IB	Avg facet/avg eruption
Cryptomys mechowi	163994	Chisel-tooth	n/a	4.86	4.58	n/a	n/a	5.12	4.64	n/a	n/a	n/a	10.69	0.4312	n/a
Heterocephalus glaber	139184	Chisel-tooth	129	1.42	1.46	4.92	2.87	1.39	1.45	4.89	2.83	153	3.08	0.4724	0.5810
Heterocephalus glaber	139185	Chisel-tooth	136	1.46	1.49	4.38	2.65	1.46	1.49	3.3	2.25	148	3.09	0.4822	0.6380
Heterocephalus glaber	147690	Chisel-tooth	125	1.3	1.38	2.87	2.47	1.3	1.38	3.96	3.18	152	2.93	0.4709	0.8272
Heliophobius argenteocinereus	79412	Chisel-tooth	141	2.07	2.14	5.1	4.14	2.07	2.12	5.05	4.09	155	4.51	0.4722	0.8108
Heliophobius argenteocinereus	79413	Chisel-tooth	131	1.33	1.51	5.13	3.28	1.35	1.5	4.99	3.29	155	3.26	0.4616	0.6492
Tachyoryctes splendens	41126	Chisel-tooth	117	1.94	2.17	5.62	3.3	1.97	2.15	5.72	3.27	157	4.35	0.4965	0.5793
Tachyoryctes splendens	41125	Chisel-tooth	117	2.35	2.33	5.79	4.1	2.38	2.38	5.76	4.19	155	5.27	0.4468	0.7177
Cannomys badius	79362	Chisel-tooth	131	2.88	2.93	4.95	5.58	2.89	2.91	4.57	5.25	143	6.63	0.4404	1.1376
Cannomys badius	79363	Chisel-tooth	125	3.12	3.02	6.07	5.85	3.14	2.96	6.06	5.95	155	6.8	0.4397	0.9727
Rhizomys pruinosus pruinosus	79361	Chisel-tooth	104	4.18	4.93	12.04	7.32	4.33	4.95	12.23	7.74	144	9.63	0.5129	0.6205
Thomomys bottae winthropi	23224	Chisel-tooth	109	2.92	2.87	7.81	6.97	2.89	2.81	7.64	6.92	154	6.38	0.4451	0.8990

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Avg length/IB	Avg facet/avg eruption
Thomomys bottae winthropi	23225	Chisel-tooth	110	2.65	2.69	6.47	5.58	2.66	2.69	6.82	5.5	154	6.01	0.4475	0.8337
Thomomys sp.	DAE 622	Chisel-tooth	100	1.34	1.27	2.93	1.25	1.37	1.26	2.94	1.25	159	3.05	0.4147	0.4258
Cryptomys hottentotus	102223	Chisel-tooth	130	1.87	1.91	3.75	3.84	1.89	1.88	4.85	5.12	148	4.48	0.4229	1.0418
Cryptomys hottentotus natalensis	135674	Chisel-tooth	129	2.42	2.54	6.25	4.45	2.44	2.54	6.04	4.4	158	5.41	0.4695	0.7200
Cryptomys hottentotus	79411	Chisel-tooth	134	2.8	2.85	8.86	5.35	2.81	2.86	9.18	5.33	158	6.37	0.4481	0.5920
Cryptomys hottentotus darlingi	134607	Chisel-tooth	137	2.13	2.01	n/a	n/a	2.12	2	3.85	2.91	154	4.57	0.4387	0.7558
Cryptomys hottentotus damariensis	41314	Chisel-tooth	139	2.6	2.37	4.86	4.51	2.6	2.35	4.55	4.51	159	5.72	0.4125	0.9585
Cryptomys hottentotus damariensis	41313	Chisel-tooth	139	2.52	2.32	3.47	2.45	2.52	2.28	3.53	2.44	146	5.5	0.4181	0.6985
Cryptomys hottentotus	18507	Chisel-tooth	129	2.17	1.92	4.17	3.24	2.14	1.88	4.23	3.19	155	4.46	0.4260	0.7654
Arvicola terrestris	121372	Chisel-tooth	100	1.83	2.11	6.67	3.37	1.81	2.1	n/a	n/a	156	3.85	0.5467	0.5052

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Avg length/IB	Avg facet/avg eruption
Arvicola terrestris	117054	Chisel-tooth	114	2.03	2.14	3.83	3.34	2.01	2.09	3.87	3.31	141	4.26	0.4964	0.8636
Arvicola terrestris	64588	Chisel-tooth	121	2.01	1.97	2.58	2.21	2.03	1.93	2.69	2.33	145	4.54	0.4295	0.8614
Ctenomys sylvanus	79402	Chisel-tooth	113	2.48	2.37	4.52	4.07	2.4	2.37	4.48	4.11	145	5.59	0.4239	0.9088
Ctenomys frater	79403	Chisel-tooth	108	2.04	1.99	3.86	2.55	2.06	2.01	3.76	2.26	156	4.71	0.4246	0.6312
Ctenomys lewisi	79399	Chisel-tooth	118	3.8	2.74	5.64	2.18	3.82	2.75	5.47	2.1	148	8.24	0.3331	0.3852
Ctenomys mendocinus	79400	Chisel-tooth	109	1.66	1.74	3.18	2.15	1.66	1.76	3.11	2.11	155	3.52	0.4971	0.6772
Ctenomys mendocinus	79401	Chisel-tooth	108	1.82	1.93	3.47	2.41	1.81	1.94	3.5	2.42	147	4.16	0.4651	0.6929
Ctenomys rionegrensis	79404	Chisel-tooth	110	2.48	2.55	5.42	3.01	2.47	2.54	5.52	2.98	140	5.63	0.4520	0.5475
Ctenomys rionegrensis	79405	Chisel-tooth	110	2.56	2.35	5.12	2.8	2.55	2.37	5.1	2.86	143	5.54	0.4259	0.5538
Ctenomys rionegrensis	79406	Chisel-tooth	120	2.48	2.3	5.37	2.99	2.48	2.28	5.34	2.91	146	5.69	0.4024	0.5508
Octodon degus	158289	Chisel-tooth	110	1.55	1.91	3.15	1.99	1.54	1.89	3.11	1.96	148	3.43	0.5539	0.6309
Octodon degus	158290	Chisel-tooth	114	1.61	2.15	3.81	1.43	1.6	2.1	3.83	1.4	134	3.8	0.5592	0.3704

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Avg length/IB	Avg facet/avg eruption
Octodon degus	158291	Chisel-tooth	106	1.65	2.03	3.58	1.59	1.67	2.02	3.55	1.58	149	3.62	0.5593	0.4446
Octodon degus	158292	Chisel-tooth	112	1.72	2.07	2.97	1.71	1.75	2.09	3.12	1.76	150	3.98	0.5226	0.5697
Octodon degus	158293	Chisel-tooth	110	1.66	2.09	2.57	1.18	1.66	2.07	2.56	1.05	150	3.86	0.5388	0.4346
Octodon degus	158294	Chisel-tooth	110	1.56	2	3.33	1.87	1.57	2.05	3.22	1.81	122	3.49	0.5802	0.5618
Octodon degus	158295	Chisel-tooth	119	1.57	1.98	2.88	1.94	1.58	1.99	2.68	1.76	144	3.48	0.5704	0.6654
Ellobius talpinus	139454	Chisel-tooth (+head-lift)	127	1.69	1.47	4.34	3.51	1.69	1.46	4.29	3.47	148	3.73	0.3927	0.8088
Spalax microphthalmus	95145	Head-lift	n/a	2.18	2.1	n/a	n/a	2.16	2.11	n/a	n/a	n/a	5.16	0.4079	n/a
Nannospalax (*Spalax*) *leucodon*	102079	Head-lift	109	1.96	2.5	n/a	n/a	2.04	2.43	4.72	5.1	173	5.05	0.4881	1.0805
Nannospalax (*Spalax*) *leucodon*	102078	Head-lift	107	2.07	2.48	n/a	n/a	2.05	2.44	4.06	4.72	168	5.05	0.4871	1.1625
Nannospalax (*Spalax*) *leucodon*	138402	Head-lift	116	2.75	2.96	3.22	5.39	2.76	3.02	3.18	5.36	166	6.39	0.4679	1.6796
Myospalax myospalax	145988	Head-lift	94	2.01	2.2	2.35	3.11	2.02	2.2	2.57	3.07	177	4.87	0.4517	1.2560
Eospalax fontanieri kukunoriensis	139553	Head-lift	106	2.14	2.5	3.93	4.04	2.15	2.45	3.58	4.32	168	4.8	0.5156	1.1131
Myospalax baileyi kukunoriensis	139557	Head-lift	105	2.3	2.46	3.86	4.16	2.34	2.5	3.78	4.31	175	5.2	0.4769	1.1086

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Avg length/IB	Avg facet/avg eruption
Myospalax baileyi kukunoriensis	139554	Head-lift	107	1.8	2.03	3.76	3.81	1.77	2.02	n/a	n/a	170	4.4	0.4602	1.0132
Aplodontia rufa rufa	14408	Scratch	107	3.86	4.26	7.97	5.83	3.89	4.23	8.66	6.29	159	10.11	0.4198	0.7288
Aplodontia rufa rufa	14409	Scratch	104	4.02	4.41	8.84	7.3	4.07	4.33	8.75	7.29	152	9.89	0.4418	0.8294
Aplodontia rufa rufa	32020	Scratch	104	3.68	4.09	7.72	6.32	3.55	4.07	7.35	6.35	153	9.82	0.4154	0.8407
Aplodontia rufa rufa	32021	Scratch	105	3.57	3.58	6.35	5.53	3.52	3.66	6.26	5.58	157	8.18	0.4425	0.8810
Aplodontia rufa pacifica	139858	Scratch	109	3.83	4.21	9.62	7.65	3.89	4.09	8.51	7.64	145	8.84	0.4694	0.8433
Aplodontia rufa pacifica	145939	Scratch	110	3.72	3.72	9.12	7.62	3.64	3.72	9.08	7.66	150	8.4	0.4428	0.8395
Aplodontia rufa pacifica	143976	Scratch	105	3.57	3.92	7.53	6.12	3.61	3.85	7.38	6.01	153	8.55	0.4543	0.8135
Aplodontia rufa pacifica	143977	Scratch	105	3.45	3.79	7.94	6.16	3.42	3.74	7.79	6.11	154	8.65	0.4352	0.7800
Bathyergus suillus	163992	Scratch	111	4.04	4.3	21.97	11.3	4.12	4.23	21.95	11.13	157	8.71	0.4896	0.5107
Bathyergus suillus	79414	Scratch	107	4.38	4.17	n/a	n/a	4.37	4.15	8.99	7.25	156	9.57	0.4346	0.8064
Geomys sp.	BAS #12	Scratch	98	2.95	3.22	7.46	6.36	2.98	3.18	7.25	6.5	154	6.52	0.4907	0.8742
Geomys bursarius	RKH #9	Scratch	103	3.49	3.39	6.97	6.03	3.42	3.32	n/a	n/a	153	7.31	0.4589	0.8651
Sigmodon hispidus texianus	163922	Scratch	97	1.51	2.33	3.95	2.82	1.51	2.24	3.92	2.82	160	3.68	0.6209	0.7166

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Avg length/IB	Avg facet/avg eruption
Sigmodon hispidus texianus	163879	Scratch	97	1.49	2.09	3.31	2.56	1.47	2.09	3.31	2.52	157	3.45	0.6057	0.7673
Castor canadensis missouriensis	81772	Scratch	101	8.62	8.85	13.67	11.38	8.56	8.97	13.37	11.37	145	18.52	0.4811	0.8413
Castor canadensis missouriensis	81870	Scratch	106	8.51	8.23	13.67	10.4	8.56	8.27	13.48	10.58	155	18.52	0.4454	0.7727
Microtus californicus californics	63292	Scratch	104	1.24	1.45	2.62	2.22	1.26	1.43	2.63	2.19	146	2.83	0.5088	0.8400
Microtus californicus californicus	47462	Scratch	100	1.38	1.78	3.12	2.09	1.41	1.78	3.08	2.06	164	3.09	0.5760	0.6693
Cynomys gunnisoni zuniensis	145454	Scratch	100	2.03	2.96	5.97	3.51	2.04	2.98	5.93	3.51	161	4.98	0.5963	0.5899
Cynomys gunnisoni zuniensis	126895	Scratch	97	1.99	3.03	7.54	5.86	1.97	3.05	6.25	5.85	157	4.97	0.6116	0.8491
Marmota monax bunkeri	3911	Scratch	110	4.75	5.91	8.19	9.44	4.74	5.87	7.99	9.64	157	12.36	0.4765	1.1792
Marmota monax bunkeri	3922	Scratch	107	4.81	6.27	11.15	9.65	4.8	6.27	10.83	9.6	162	12.02	0.5216	0.8757
Marmota flaviventris nosophora	32349	Scratch	104	3.86	5.08	9.54	7.42	3.87	5.07	9.54	7.42	155	10.4	0.4879	0.7777
Marmota flaviventris nosophora	19954	Scratch	101	4.81	6.95	8.59	10.08	4.85	6.95	8.36	9.67	159	11.45	0.6069	1.1651

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Avg length/IB	Avg facet/avg eruption
Spermophilus tridecemlineatus tridecemlineatus	144027	Scratch	100	1.44	2.14	3.14	2.29	1.44	2.13	3.16	2.27	156	3.42	0.6242	0.7238
Citellus tridecemlineatus tridecemlineatus	46058	Scratch	92	1.29	2.3	4.25	2.93	1.28	2.33	4.24	2.93	163	3.32	0.6972	0.6902
Tamias palmeri	132240	Scratch	101	1.04	1.76	3.57	2.13	1.04	1.79	3.56	2	156	2.62	0.6774	0.5792
Tamias palmeri	132248	Scratch	96	1.08	1.86	3.07	1.85	1.08	1.91	3.11	1.78	165	2.98	0.6325	0.5873
Pappogeomys bulleri albinasus	31015	Scratch	98	2.65	2.95	7.36	5.8	2.68	2.92	7.07	5.04	158	6.07	0.4835	0.7512
Pappogeomys bulleri albinensis	31016	Scratch	99	2.28	2.62	6.42	5.01	2.32	2.59	6.21	4.97	159	5.38	0.4842	0.7901
Orthogeomys heterodus cartogoensis	142722	Scratch	103	3.93	3.43	6.73	5.07	3.95	3.48	6.67	4.82	162	9.2	0.3755	0.7380
Orthogeomys heterodus	158449	Scratch	100	3.46	3.22	6.37	6.32	3.46	3.11	6.24	6.65	158	7.96	0.3976	1.0285
Cratogeomys castanops	116697	Scratch	94	3.75	4.1	12.82	8.87	3.76	3.99	12.59	8.99	152	8.69	0.4654	0.7028
Cratogeomys castanops	116695	Scratch	100	2.93	3.1	9.13	6.89	2.91	3.06	8	5.73	150	6.76	0.4556	0.7367

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Incisor breath (IB) (mm)	Avg length/IB	Avg facet/avg eruption
Geomys bursarius	JMT #17	Scratch	103	2.86	2.81	7.21	6.54	2.9	2.79	7.21	6.06	155	6.74	0.4154	0.8737
Geomys bursarius	JPP #5	Scratch	94	3.11	2.89	5.7	5.86	3.13	2.89	5.76	5.85	161	6.96	0.4152	1.0218
Geomys bursarus	GLT #17	Scratch	96	3.21	3.23	6.95	6.55	3.22	3.28	6.97	6.58	161	7.3	0.4458	0.9432
Geomys bursarus	RAK #13	Scratch	97	3.12	3.31	7.82	8	3.14	3.33	7.86	8.03	155	7.25	0.4579	1.0223
Geomys bursarus	JAI #13	Scratch	100	3.69	3.41	7.28	7.17	3.71	3.41	6.96	6.49	156	8.43	0.4045	0.9592
Geomys bursarus	JLA #9	Scratch	100	3.11	2.96	5.43	4.95	3.13	2.94	5.43	4.91	155	6.91	0.4269	0.9079
Geomys bursarus	RSJ #13	Scratch	102	3.02	2.82	7.13	5.39	3.07	2.78	6.75	5.24	155	6.66	0.4204	0.7658
Geomys bursarus	FSB #9	Scratch	100	3.72	3.63	6.39	6.53	3.79	3.69	6.13	6.45	157	8.21	0.4457	1.0367

Appendix VIII. Lower Incisor Measurements of Modern Rodents

Taxon	KU Number	Habit	Procumbency (°)	incisor width	incisor length	eruption length	facet length	incisor width	incisor length	eruption length	facet length	Facet angle (°)	Avg width/Avg length	Avg facet/avg eruption
Cryptomys mechowi	163994	Chisel-tooth	117	4.38	4.86	13.02	6.88	4.39	4.88	13.29	6.93	140	0.9004	0.5248
Heterocephalus glaber	139184	Chisel-tooth	116	1.15	1.56	6.27	3.08	1.12	1.52	6.27	3.13	150	0.7370	0.4952
Heterocephalus glaber	139185	Chisel-tooth	117	1.15	1.56	5.34	3.22	1.15	1.57	5.37	3.22	148	0.7348	0.6013
Heterocephalus glaber	147690	Chisel-tooth	124	n/a	n/a	n/a	n/a	1.08	1.48	5.08	3.24	149	0.7297	0.6377
Heliophobius argenteneoceres	79412	Chisel-tooth	127	2.07	2.41	7.81	5.42	2.04	2.44	7.7	5.42	163	0.8474	0.6989
Heliophobius argenteneoceres	79413	Chisel-tooth	134	1.31	1.7	5.59	3.1	1.29	1.71	5.59	3.18	145	0.7624	0.5617
Tachyoryctes splendens	41126	Chisel-tooth	115	1.89	2.01	9.25	4.63	1.83	1.93	9.23	4.63	158	0.9441	0.5010
Tachyoryctes splendens	41125	Chisel-tooth	116	2.08	2.26	9.02	6.77	2.09	2.27	9.65	6.74	162	0.9205	0.7236
Cannomys badius	79362	Chisel-tooth	113	3.05	3.46	11.98	9.13	3	3.44	11.65	8.99	138	0.8768	0.7668
Cannomys badius	79363	Chisel-tooth	111	3.09	3.36	10.11	6.45	3.05	3.35	10.14	6.48	158	0.9150	0.6385
Thomomys bottae winthropi	23224	Chisel-tooth	112	2.83	3.22	10.39	7.8	2.81	3.2	10.37	7.72	162	0.8785	0.7475
Thomomys bottae winthropi	23225	Chisel-tooth	120	2.6	2.99	9.58	6.04	2.64	3.04	9.08	5.75	168	0.8689	0.6318
Cryptomys hottentotus	102223	Chisel-tooth	119	2.06	2.31	9.23	6.19	2.06	2.3	9.02	6.16	162	0.8937	0.6767
Cryptomys hottentotus natalensis	135674	Chisel-tooth	125	2.58	2.83	10.98	5.63	2.59	2.79	10.73	5.49	158	0.9199	0.5122
Cryptomys hottentotus	79411	Chisel-tooth	121	2.82	3.32	13.24	4.58	2.79	3.32	11.97	4.55	148	0.8448	0.3621
Cryptomys hottentotus darlingi	134607	Chisel-tooth	126	2.04	2.45	8.85	2.69	2.03	2.45	8	3.59	165	0.8306	0.3727
Cryptomys hottentotus damariensis	41314	Chisel-tooth	116	2.4	2.67	8.39	4.96	2.41	2.69	8.48	4.97	165	0.8973	0.5886

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Avg width/Avg length	Avg facet/avg eruption
Cryptomys hottentotus damariensis	41313	Chisel-tooth	122	2.05	2.58	8.62	5.13	2.11	2.57	8.69	5.19	166	0.8077	0.5961
Cryptomys hottentotus	18507	Chisel-tooth	133	1.92	2.16	6.9	5.85	1.93	2.14	6.83	5.81	165	0.8953	0.8492
Arvicola terrestris	121372	Chisel-tooth	115	n/a	n/a	n/a	n/a	1.57	1.84	7.8	5.64	163	0.8532	0.7230
Arvicola terrestris	64588	Chisel-tooth	109	1.72	2	8.19	5.82	1.76	2.01	8.22	5.66	167	0.8678	0.6995
Ctenomys sylvanus	79402	Chisel-tooth	121	2.32	2.55	6.21	3.55	2.34	2.53	6.18	3.67	159	0.9173	0.5827
Ctenomys frater	79403	Chisel-tooth	121	1.84	1.83	3.62	3.92	1.85	1.82	3.73	3.63	151	1.0109	1.0272
Ctenomys lewisi	79399	Chisel-tooth	113	3.38	2.81	11.12	5.56	3.39	2.78	11.08	5.52	167	1.2110	0.4990
Ctenomys mendocinus	79400	Chisel-tooth	113	1.7	1.78	4.64	3.28	1.71	1.75	4.56	3.25	169	0.9660	0.7097
Ctenomys mendocinus	79401	Chisel-tooth	116	1.9	1.97	5.27	3.46	1.93	1.96	5.3	3.42	160	0.9745	0.6508
Ctenomys rionegrensis	79404	Chisel-tooth	116	2.43	2.46	6.08	3.83	2.43	2.46	n/a	n/a	156	0.9878	0.6299
Ctenomys rionegrensis	79405	Chisel-tooth	113	2.47	2.26	5.8	3.1	2.44	2.28	5.81	3.19	150	1.0814	0.5417
Ctenomys rionegrensis	79406	Chisel-tooth	111	2.45	2.28	5.8	3.88	2.49	2.24	5.8	3.8	162	1.0929	0.6620

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Avg width/Avg length	Avg facet/avg eruption
Aconaemys fuscus	79398	Chisel-tooth	102	1.41	1.64	4.62	3.54	1.41	1.61	4.54	3.52	161	0.8676	0.7707
Octodon degus	158289	Chisel-tooth	128	1.36	1.87	4.81	2.6	1.35	1.85	4.65	2.55	155	0.7284	0.5443
Octodon degus	158290	Chisel-tooth	119	1.46	2.01	5.01	2.84	1.48	2.01	5.04	2.84	149	0.7313	0.5651
Octodon degus	158291	Chisel-tooth	129	1.47	1.99	4.54	2.22	1.43	1.99	4.66	2.49	156	0.7286	0.5119
Octodon degus	158292	Chisel-tooth	120	1.51	1.95	5.86	2.91	1.49	1.92	5.68	2.93	150	0.7751	0.5060
Octodon degus	158293	Chisel-tooth	130	1.54	2.03	4.74	2.65	1.49	2.03	4.74	2.72	159	0.7463	0.5664
Octodon degus	158294	Chisel-tooth	120	1.41	1.88	4.94	3.52	1.43	1.84	5.1	3.53	152	0.7634	0.7021
Octodon degus	158295	Chisel-tooth	123	1.49	1.95	5.15	3.8	1.49	1.94	4.92	3.56	168	0.7660	0.7308
Ellobius talpinus	139454	Chisel-tooth (+head-lift)	116	1.35	1.73	7.7	5.1	1.44	1.77	7.4	5.1	165	0.9529	0.8088
Nannospalax (*Spalax*) *leucodon*	102079	Head-lift	116	2.21	2.83	n/a	n/a	2.16	2.73	11.84	7.81	164	0.7859	0.6596
Nannospalax (*Spalax*) *leucodon*	102078	Head-lift	125	2.11	2.92	11.54	7.74	2.1	2.9	11.52	7.79	166	0.7233	0.6734
Nannospalax (*Spalax*) *leucodon*	138402	Head-lift	128	2.94	3.16	7.5	8.27	2.94	3.14	7.53	8.32	167	0.9333	1.1037

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Avg width/Avg length	Avg facet/avg eruption
Spalax microphthalmus	95145	Head-lift	128	2.18	1.97	8.05	5.36	2.21	1.98	8.08	5.5	155	1.1113	0.6732
Myospalax myospalax	145988	Head-lift	120	1.84	2.22	5.33	3.85	1.81	2.24	5.44	4.17	166	0.8183	0.7446
Eospalax fontanieri kukunoriensis	139553	Head-lift	120	1.84	2.47	7.15	5.44	1.88	2.47	7.15	5.41	166	0.7530	0.7587
Myospalax baileyi kukunoriensis	139557	Head-lift	121	1.84	2.53	6.33	4.73	1.86	2.53	7.17	5.12	175	0.7312	0.7296
Myospalax baileyi kukunoriensis	139554	Head-lift	117	1.48	1.93	5.75	4.16	1.5	1.79	5.73	4.14	174	0.8010	0.7229
Aplodontia rufa rufa	14408	Scratch	126	3.73	4.3	9.83	7.28	3.74	4.3	10.32	7.73	153	0.8686	0.7449
Aplodontia rufa rufa	14409	Scratch	125	3.56	4.25	9.51	9.51	3.58	4.32	9.58	9.25	149	0.8331	0.9827
Aplodontia rufa rufa	32020	Scratch	124	3.83	4.52	10.57	7.49	3.91	4.48	10.43	7.47	155	0.8600	0.7123
Aplodontia rufa rufa	32021	Scratch	124	3.49	4.08	9.3	5.65	3.47	4.07	9.51	6.83	157	0.8539	0.6634
Aplodontia rufa pacifica	139858	Scratch	118	3.76	4.69	10.94	9.97	3.76	4.67	11.17	10.36	148	0.8034	0.9194
Aplodontia rufa pacifica	145939	Scratch	124	3.57	3.82	12.62	8.73	3.58	3.81	12.62	8.91	152	0.9370	0.6988
Aplodontia rufa pacifica	143976	Scratch	117	3.51	4.22	12.3	7.52	3.55	4.26	12.77	7.52	152	0.8325	0.5999
Aplodontia rufa pacifica	143977	Scratch	120	3.11	3.77	11.35	8.19	3.11	3.79	11.55	8.39	153	0.8227	0.724

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Avg width/Avg length	Avg facet/avg eruption
Bathyergus suillus	163992	Scratch	116	3.58	6.47	22.64	11.54	3.57	6.46	22.58	11.54	161	0.5529	0.5103
Bathyergus suillus	79414	Scratch	113	4.05	6.18	12.98	10.05	3.97	6.21	23.47	10.05	141	0.6472	0.5514
Geomys sp.	BAS #12	Scratch	118	2.89	3.06	10.91	5.11	2.84	3.07	10.71	5.11	152	0.9347	0.4727
Geomys bursarius	RKH #9	Scratch	122	3.35	3.46	9.38	6.49	3.31	3.47	9.55	4.61	147	0.9610	0.5863
Sigmodon hispidus texianus	163922	Scratch	123	1.49	1.87	5.61	4.57	1.49	1.83	5.54	4.69	165	0.8054	0.8304
Sigmodon hispidus texianus	163879	Scratch	122	1.38	1.85	4.62	4.03	1.37	1.85	4.65	4.01	157	0.7432	0.8673
Castor canadensis missouriensis	81772	Scratch	110	8.43	10.11	21.02	14.87	8.47	n/a	n/a	n/a	160	0.8358	0.7074
Castor canadensis missouriensis	81870	Scratch	113	8.41	8.94	19.05	15.69	8.28	8.95	19.01	15.65	152	0.9329	0.8234
Microtus californicus californics	63292	Scratch	123	1.05	1.32	3.58	2.32	1.06	1.33	3.53	2.35	167	0.7962	0.6568
Microtus californicus californicus	47462	Scratch	127	1.14	1.29	3.75	3.97	1.14	1.33	3.74	4	164	0.8702	1.0640
Cynomys gunnisoni zuniensis	145454	Scratch	133	1.88	2.93	7.63	6.1	1.9	2.94	7.42	6.06	165	0.6439	0.8079
Cynomys gunnisoni zuniensis	126895	Scratch	129	1.94	2.89	9.02	6.1	1.94	2.87	9.02	6.11	146	0.6736	0.6768

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Avg width/Avg length	Avg facet/avg eruption
Marmota monax bunkeri	3911	Scratch	122	4.51	5.92	11.44	9.86	4.59	6.24	10.95	9.49	162	0.7483	0.8642
Marmota monax bunkeri	3922	Scratch	120	4.52	5.63	14.22	9.66	4.54	5.56	14.27	10.24	146	0.8096	0.6984
Marmota flaviventris nosophora	32349	Scratch	121	3.57	4.74	15.03	8.8	3.47	4.74	15.97	8.85	158	0.7426	0.5693
Marmota flaviventris nosophora	19954	Scratch	121	4.23	6.17	15.37	12.14	4.27	6.15	15.42	12.64	146	0.6899	0.8048
Spermophilus tridecemlineatus tridecemlineatus	144027	Scratch	126	1.15	1.71	5.99	4.18	1.14	1.69	5.98	4.18	143	0.6735	0.6984
Citellus tridecemlineatus tridecemlineatus	46058	Scratch	130	1.18	1.88	6.25	4.96	1.18	1.86	6.19	4.9	152	0.6310	0.7926
Tamias palmeri	132240	Scratch	134	0.92	1.6	4.15	3.14	0.97	1.62	4.13	3.15	149	0.5869	0.7596
Tamias palmeri	132248	Scratch	147	1.05	1.7	2.33	1.5	1.02	1.67	1.98	1.24	156	0.6142	0.6357
Pappogeomys bulleri albinasus	31015	Scratch	105	2.48	2.89	9.15	5.56	2.53	2.91	8.5	5.37	160	0.8637	0.6192
Pappogeomys bulleri albinensis	31016	Scratch	110	2.26	2.5	7.31	5.25	2.21	2.54	7.47	5.68	158	0.8869	0.7395
Orthogeomys heterodus cartogoensis	142722	Scratch	102	3.83	3.36	12.3	5.68	3.81	3.36	11.71	5.51	165	1.1369	0.4660

Taxon	KU Number	Habit	Procumbency (°)	Left incisor width (mm)	Left incisor length (mm)	Left eruption length (mm)	Left facet length (mm)	Right incisor width (mm)	Right incisor length (mm)	Right eruption length (mm)	Right facet length (mm)	Facet angle (°)	Avg width/Avg length	Avg facet/avg eruption
Orthogeomys heterodus	158449	Scratch	111	3.35	3.17	9.23	7.12	3.33	3.23	8.57	7.45	163	1.0437	0.8185
Cratogeomys castanops	116697	Scratch	113	3.68	3.7	13.12	9.29	3.65	3.76	13.4	9.48	165	0.9825	0.7077
Cratogeomys castanops	116695	Scratch	107	2.66	2.67	9.92	7.87	2.71	2.68	9.61	7.45	168	1.0037	0.7844
Geomys bursarius	JMT #17	Scratch	111	3.03	2.68	7.62	6.19	2.97	2.71	7.63	6.25	167	1.1131	0.8157
Geomys bursarius	JPP #5	Scratch	113	3.04	2.74	8.31	6.58	3.03	2.71	8.43	6.47	154	1.1137	0.7795
Geomys bursarius	GLT #17	Scratch	118	3	3.32	8.92	3.48	3.02	3.33	8.82	3.38	162	0.9052	0.3866
Geomys bursarius	RAK #13	Scratch	106	3.16	3.31	10.96	7.52	3.18	3.31	10.81	7.49	122	0.9577	0.6894
Geomys bursarius	JAI #13	Scratch	113	3.45	3.191	10.44	7.14	3.42	3.221	10.26	6.6	139	1.0714	0.6637
Geomys bursarius	JLA #9	Scratch	110	3.04	2.97	8.27	5.12	3	2.94	8.27	5.22	140	1.0219	0.6251
Geomys bursarius	RSJ #13	Scratch	106	3.04	2.84	10.69	4.75	3.03	2.85	10.95	4.88	150	1.0667	0.4450
Geomys bursarius	FSB #9	Scratch	118	3.58	3.56	7.15	4.34	3.56	3.55	7.64	4.84	145	1.0042	0.6206

Appendix IX. Upper Incisor Wear Patterns in Modern Rodents

Taxon	KU Number	Habit	Incisor wear	Upper incisor groove?
Cryptomys mechowi	163994	Chisel-tooth	n/a	no
Heterocephalus glaber	139184	Chisel-tooth	concave	no
Heterocephalus glaber	139185	Chisel-tooth	left incisor slightly convex, right incisor angles down to midline with a slight concavity	faint
Heterocephalus glaber	147690	Chisel-tooth	right incisor convex, left incisor angles down to midline	faint
Heliophobius argenteocinereus	79412	Chisel-tooth	flat with rounded edges	no
Heliophobius argenteocinereus	79413	Chisel-tooth	flat with rounded edges	no
Tachyoryctes splendens	41126	Chisel-tooth	flat	no
Tachyoryctes splendens	41125	Chisel-tooth	flat with rounded edges	no
Cannomys badius	79362	Chisel-tooth	slightly convex with point highly skwed to midline	no
Cannomys badius	79363	Chisel-tooth	flat, but angled down toward midline	no
Rhizomys pruinosus pruinosus	79361	Chisel-tooth	angled slightly down to midline	no
Thomomys bottae winthropi	23224	Chisel-tooth	convex with point skewed to lateral edge	no
Thomomys bottae winthropi	23225	Chisel-tooth	slopes up to the midline	no
Thomomys sp.	DAE 622	Chisel-tooth	angled up towards midline	no
Cryptomys hottentotus	102223	Chisel-tooth	flat	no
Cryptomys hottentotus natalensis	135674	Chisel-tooth	concave	no
Cryptomys hottentotus	79411	Chisel-tooth	left is flat, higher medially, right is concave	no
Cryptomys hottentotus darlingi	134607	Chisel-tooth	convex, tip is broad and medial; left broken	no
Cryptomys hottentotus damariensis	41314	Chisel-tooth	flat	no

Cryptomys hottentotus damariensis	41313	Chisel-tooth	convex, point is central to each incisor	no
Cryptomys hottentotus	18507	Chisel-tooth	concave	No
Arvicola terrestris	121372	Chisel-tooth	slope down laterally	no
Arvicola terrestris	117054	Chisel-tooth	concave	no
Arvicola terrestris	64588	Chisel-tooth	concave but medial end lower than lateral end	no
Ctenomys sylvanus	79402	Chisel-tooth	flat	faint
Ctenomys frater	79403	Chisel-tooth	flat	no
Ctenomys lewisi	79399	Chisel-tooth	flat with rounded lateral edge, right incisor somewhat indented from lower incisor	no
Ctenomys mendocinus	79400	Chisel-tooth	right incisor concave, left incisor primarily angled downward toward midline & with slight concavity toward midline	no
Ctenomys mendocinus	79401	Chisel-tooth	both incisors slightly concave but angled down toward midline	no
Ctenomys rionegrensis	79404	Chisel-tooth	flat	no
Ctenomys rionegrensis	79405	Chisel-tooth	flat	no
Ctenomys rionegrensis	79406	Chisel-tooth	slants down toward midline	no
Octodon degus	158289	Chisel-tooth	convex with higher medial edge	no
Octodon degus	158290	Chisel-tooth	concave	no
Octodon degus	158291	Chisel-tooth	worn lower toward midline	no
Octodon degus	158292	Chisel-tooth	right incisor slants upward toward midline, left is flat	no
Octodon degus	158293	Chisel-tooth	right incisor convex, left incisor flat	no
Octodon degus	158294	Chisel-tooth	slightly concave	no
Octodon degus	158295	Chisel-tooth	concave	no
Ellobius talpinus	139454	Chisel-tooth (+head-lift)	flat with rounded edges	no
Spalax microphthalmus	95145	Head-lift	n/a	no
Nannospalax (*Spalax*) *leucodon*	102079	Head-lift	concave	faint
Nannospalax (*Spalax*) *leucodon*	102078	Head-lift	concave	faint
Nannospalax (*Spalax*) *leucodon*	138402	Head-lift	weakly concave	faint

Myospalax myospalax	145988	Head-lift	slightly concave	no
Eospalax fontanieri kukunoriensis	139553	Head-lift	right is concave, left is angled down toward midline	no
Myospalax baileyi kukunoriensis	139557	Head-lift	slightly concave	no
Myospalax baileyi kukunoriensis	139554	Head-lift	slightly concave	no
Aplodontia rufa rufa	14408	Scratch	weakly convex, point skewed toward lateral edge	faint
Aplodontia rufa rufa	14409	Scratch	convex with point strongly skewed toward lateral edge of incisor, almost appears as if the face is flat but angled on the right incisor	faint
Aplodontia rufa rufa	32020	Scratch	weakly convex, point skewed toward lateral edge, left tooth has an indenration formed by the lower incisor	faint
Aplodontia rufa rufa	32021	Scratch	weakly convex	faint
Aplodontia rufa pacifica	139858	Scratch	weakly convex, point skewed to lateral edge, right incisor almost flat in appearance	faint
Aplodontia rufa pacifica	145939	Scratch	convex, point is skewed to lateral edge, point is blunt on right tooth	faint
Aplodontia rufa pacifica	143976	Scratch	each incisor is flat, but the edge is angled upward to the midline (or convex with the point skewed entirely to the lateral edge)	faint
Aplodontia rufa pacifica	143977	Scratch	convex, point is skewed to lateral edge	no
Bathyergus suillus	163992	Scratch	serrated, faintly lower at midline than at lateral edges	yes
Bathyergus suillus	79414	Scratch	serrated, angled down toward midline	yes
Geomys sp.	BAS #12	Scratch	serrated, faintly lower at midline than at lateral edges	yes
Geomys bursarius	RKH #9	Scratch	right incisor broken, but left incisor serrated with a lower lateral edge and a higher medial edge	yes
Sigmodon hispidus texianus	163922	Scratch	serrated edge, highest points lateral	faint
Sigmodon hispidus texianus	163879	Scratch	serrated convex edge	faint
Castor canadensis missouriensis	81772	Scratch	flat to concave	no
Castor canadensis missouriensis	81870	Scratch	slightly convex	no

Microtus californicus californics	63292	Scratch	flat	no
Microtus californicus californicus	47462	Scratch	strongly concave, there is an obvious and deep notch cut by lowers	no
Cynomys gunnisoni zuniensis	145454	Scratch	convex, but flattened near medial edge where groove occurs	very faint
Cynomys gunnisoni zuniensis	126895	Scratch	serrated edge	very faint
Marmota monax bunkeri	3911	Scratch	convex on lateral half of incisor, convex on medial half (demarcated) by groove	yes
Marmota monax bunkeri	3922	Scratch	sonvex, point is lateral	yes
Marmota flaviventris nosophora	32349	Scratch	left tooth serrated, right tooth serrated and convex, major point central	yes
Marmota flaviventris nosophora	19954	Scratch	weakly convex, serrated	yes
Spermophilus tridecemlineatus tridecemlineatus	144027	Scratch	concave	no
Citellus tridecemlineatus tridecemlineatus	46058	Scratch	concave	no
Tamias palmeri	132240	Scratch	weakly convex, higher medially	no
Tamias palmeri	132248	Scratch	flat, left angled medially	no
Pappogeomys bulleri albinasus	31015	Scratch	concave, point at lateral edge	yes
Pappogeomys bulleri albinensis	31016	Scratch	flat, lateral point on left tooth	yes
Orthogeomys heterodus cartogoensis	142722	Scratch	weakly convex, but notched at groove	yes
Orthogeomys heterodus	158449	Scratch	flat with notch at groove	yes
Cratogeomys castanops	116697	Scratch	concave, teeth split along groove	yes
Cratogeomys castanops	116695	Scratch	convex, point is lateral, serrated near groove	yes
Geomys bursarius	JMT #17	scratch	serated	yes
Geomys bursarius	JPP #5	scratch	serated	yes

Geomys bursarus	GLT #17	scratch	serated	yes
Geomys bursarus	RAK #13	scratch	serated	yes
Geomys bursarus	JAI #13	scratch	serated	yes
Geomys bursarus	JLA #9	scratch	serated, forms a notch where the groove is present	yes
Geomys bursarus	RSJ #13	scratch	serated, notch where the groove is present	yes
Geomys bursarus	FSB #9	scratch	serated, highly worn;tips of both teeth together slant to the right side	yes

Appendix X. Lower Incisor Wear Patterns in Modern Rodents

Taxon	KU number	Habit	Incisor wear
Cryptomys mechowi	163994	Chisel-tooth	flat
Heterocephalus glaber	139184	Chisel-tooth	somewhat convex
Heterocephalus glaber	139185	Chisel-tooth	slightly convex
Heterocephalus glaber	147690	Chisel-tooth	flat
Heliophobius argenteneoceres	79412	Chisel-tooth	flat with rounded edges
Heliophobius argenteneoceres	79413	Chisel-tooth	slightly concave
Tachyoryctes splendens	41126	Chisel-tooth	flat, but slightly higher at midline than lateral edge
Tachyoryctes splendens	41125	Chisel-tooth	flat with rounded edges
Cannomys badius	79362	Chisel-tooth	flat with rounded lateral edge
Cannomys badius	79363	Chisel-tooth	flat
Thomomys bottae winthropi	23224	Chisel-tooth	convex, very blunt
Thomomys bottae winthropi	23225	Chisel-tooth	convex, very blunt
Cryptomys hottentotus	102223	Chisel-tooth	convex, somewhat taller medially
Cryptomys hottentotus natalensis	135674	Chisel-tooth	convex, tip is near center of each incisor
Cryptomys hottentotus	79411	Chisel-tooth	convex, tip is broad but medial
Cryptomys hottentotus darlingi	134607	Chisel-tooth	concave
Cryptomys hottentotus damariensis	41314	Chisel-tooth	flat, but angled toward midline
Cryptomys hottentotus damariensis	41313	Chisel-tooth	convex, higher medially

Cryptomys hottentotus	18507	Chisel-tooth	convex, higher medially
Arvicola terrestris	121372	Chisel-tooth	slopes upward laterally
Arvicola terrestris	64588	Chisel-tooth	strongly convex
Ctenomys sylvanus	79402	Chisel-tooth	faintly serrated
Ctenomys frater	79403	Chisel-tooth	flat
Ctenomys lewisi	79399	Chisel-tooth	faintly serrated
Ctenomys mendocinus	79400	Chisel-tooth	right flat with rounded edges, left slightly convex, both faintly serrated
Ctenomys mendocinus	79401	Chisel-tooth	right incisor concave, both incisors angled upward toward midline
Ctenomys rionegrensis	79404	Chisel-tooth	flat
Ctenomys rionegrensis	79405	Chisel-tooth	both slightly convex
Ctenomys rionegrensis	79406	Chisel-tooth	flat with rounded lateral edges
Aconaemys fuscus	79398	Chisel-tooth	slanted upward laterally
Octodon degus	158289	Chisel-tooth	convex
Octodon degus	158290	Chisel-tooth	slanted upward toward midline
Octodon degus	158291	Chisel-tooth	right incisor convex, left incisor slightly concave
Octodon degus	158292	Chisel-tooth	both incisors form a continuous surface that slopes upward to the left
Octodon degus	158293	Chisel-tooth	left incisor flat, right incisor slopes up toward midline
Octodon degus	158294	Chisel-tooth	convex
Octodon degus	158295	Chisel-tooth	convex
Ellobius talpinus	139454	Chisel-tooth (+head-lift)	slightly convex
Nannospalax (*Spalax*) *leucodon*	102079	Head-lift	convex with blunted tips
Nannospalax (*Spalax*) *leucodon*	102078	Head-lift	flattened with rounded edges
Nannospalax (*Spalax*) *leucodon*	138402	Head-lift	flattened with rounded edges
Spalax microphthalmus	95145	Head-lift	convex with point skewed toward midline
Myospalax myospalax	145988	Head-lift	convex

Eospalax fontanieri kukunoriensis	139553	Head-lift	convex
Myospalax baileyi kukunoriensis	139557	Head-lift	convex
Myospalax baileyi kukunoriensis	139554	Head-lift	convex
Aplodontia rufa rufa	14408	Scratch	convex, blunted tips
Aplodontia rufa rufa	14409	Scratch	convex, incisors are angled toward midle so medial portion of point is somewhat flattened
Aplodontia rufa rufa	32020	Scratch	convex, blunted tips
Aplodontia rufa rufa	32021	Scratch	convex, blunted tips
Aplodontia rufa pacifica	139858	Scratch	overall flat, but tips converge closely and the whole cutting edge tilts down from the higher left side to the lower right side, lateral edges of incisors are rounded
Aplodontia rufa pacifica	145939	Scratch	convex
Aplodontia rufa pacifica	143976	Scratch	convex, point skewed medially
Aplodontia rufa pacifica	143977	Scratch	convex, blunted tips, skewed medially
Bathyergus suillus	163992	Scratch	serrated overall, but angled downard toward midline
Bathyergus suillus	79414	Scratch	right flattened, left angles up toward the midline
Geomys sp.	BAS #12	Scratch	serrated
Geomys bursarius	RKH #9	Scratch	right incisor broken, left incisor serrated
Sigmodon hispidus texianus	163922	Scratch	flat, angled medially
Sigmodon hispidus texianus	163879	Scratch	right flat, left curved, both angled up to midline
Castor canadensis missouriensis	81772	Scratch	curved, highest from center to medial side
Castor canadensis missouriensis	81870	Scratch	convex
Microtus californicus californics	63292	Scratch	highly convex, points near incisor center

Microtus californicus californicus	47462	Scratch	highly convex, points are just medial of center
Cynomys gunnisoni zuniensis	145454	Scratch	weakly convex
Cynomys gunnisoni zuniensis	126895	Scratch	convex with points near lateral edge
Marmota monax bunkeri	3911	Scratch	convex with point near center of tooth
Marmota monax bunkeri	3922	Scratch	convex, point is lateral
Marmota flaviventris nosophora	32349	Scratch	weakly concave with medial point
Marmota flaviventris nosophora	19954	Scratch	convex, serrated
Spermophilus tridecemlineatus tridecemlineatus	144027	Scratch	convex, point medial
Citellus tridecemlineatus tridecemlineatus	46058	Scratch	weakly convex, broad point from center to medial edge
Tamias palmeri	132240	Scratch	flat, angled medially
Tamias palmeri	132248	Scratch	flat, right angled medially
Pappogeomys bulleri albinasus	31015	Scratch	convex, broad medial point
Pappogeomys bulleri albinensis	31016	Scratch	flat
Orthogeomys heterodus cartogoensis	142722	Scratch	convex, point at center
Orthogeomys heterodus	158449	Scratch	flat, weakly serrated
Cratogeomys castanops	116697	Scratch	flat, angled medially
Cratogeomys castanops	116695	Scratch	convex, broad medial point
Geomys bursarius	JMT #17	Scratch	serated
Geomys bursarius	JPP #5	Scratch	serated
Geomys bursarius	GLT #17	Scratch	serated the tip is higher medially than laterally

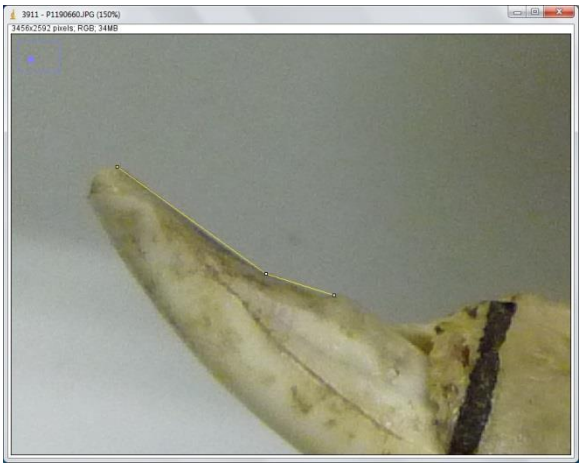
Geomys bursarius	RAK #13	Scratch	serated the tip is higher medially than laterally
Geomys bursarius	JAI #13	Scratch	serated
Geomys bursarius	JLA #9	Scratch	faintly serated
Geomys bursarius	RSJ #13	Scratch	serated
Geomys bursarius	FSB #9	Scratch	serated but highly worn;the wear on the incisors tilts down to the left

Appendix XI. ImageJ Angle Measurements for Modern Rodent Skulls

Upper Procumbency Angle

Upper Facet Angle

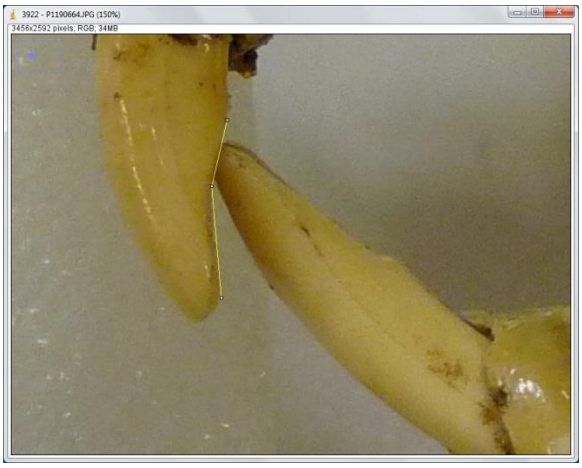
Lower Procumbency Angle



Lower Facet Angle

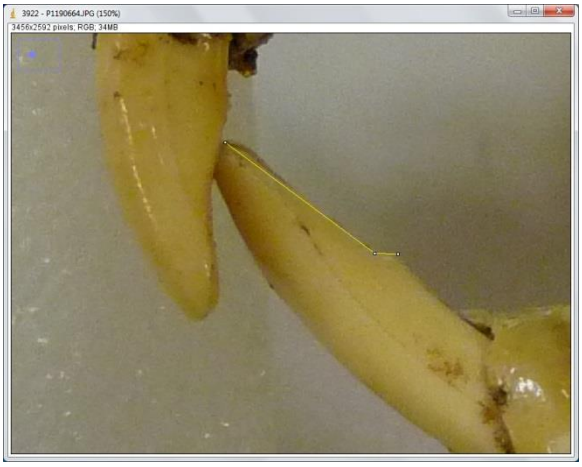
KU 3911 (*Marmota monax*)

Upper Procumbency Angle



Upper Facet Angle

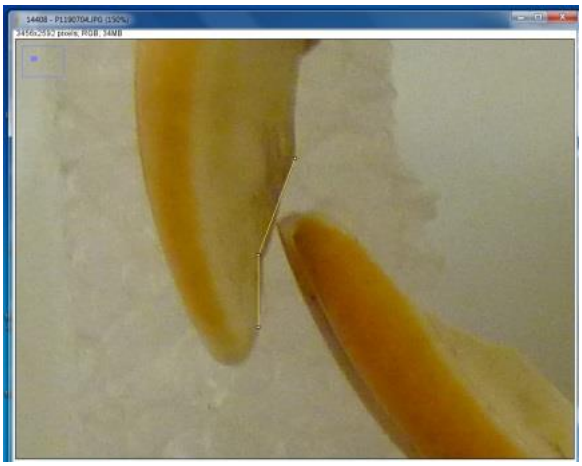
Lower Procumbency Angle



Lower Facet Angle

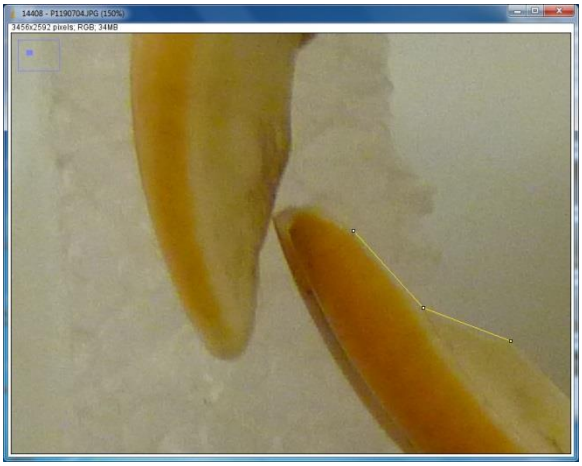
KU 3922 (*Marmota monax*)

Upper Procumbency Angle



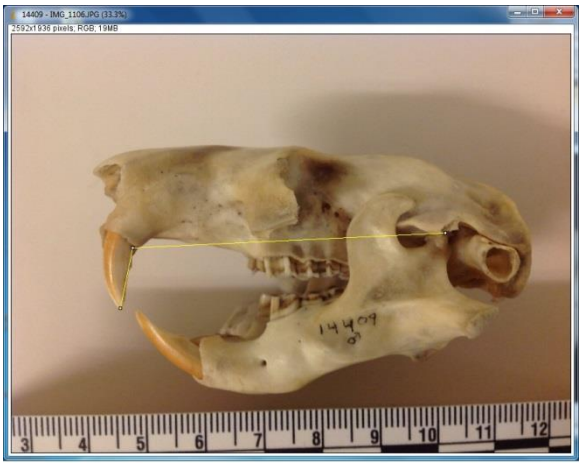
Upper Facet Angle

Lower Procumbency Angle

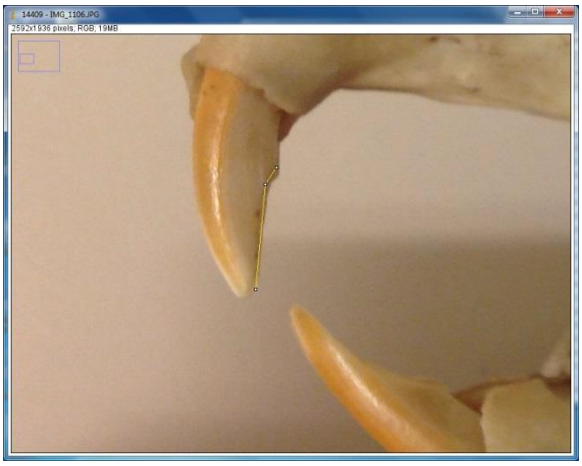


Lower Facet Angle

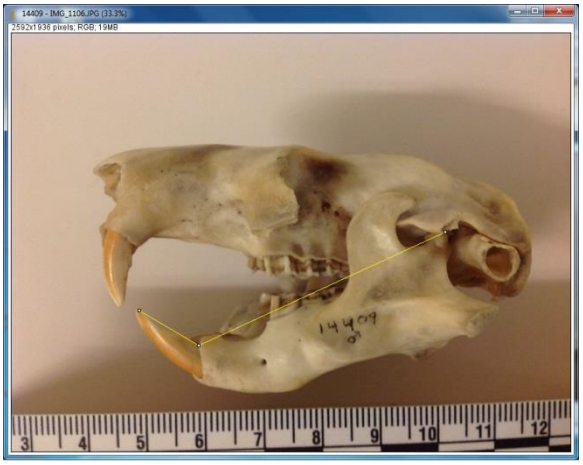
KU 14408 (*Aplodontia rufa*)



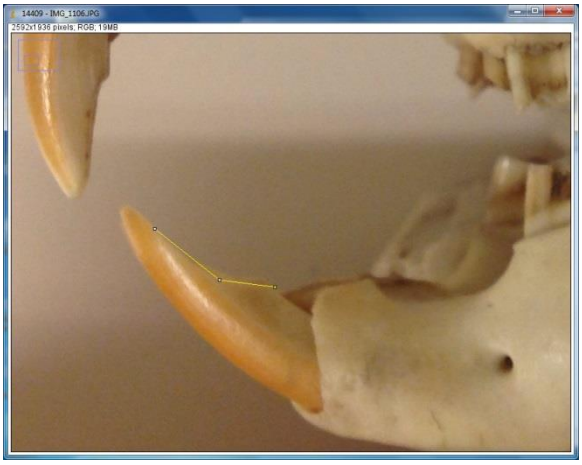
Upper Procumbency Angle



Upper Facet Angle



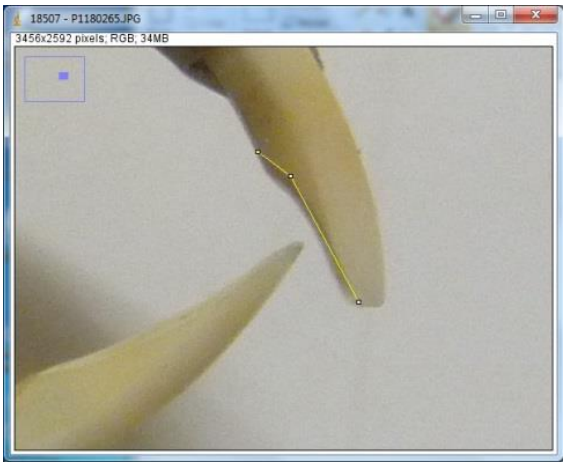
Lower Procumbency Angle



Lower Facet Angle

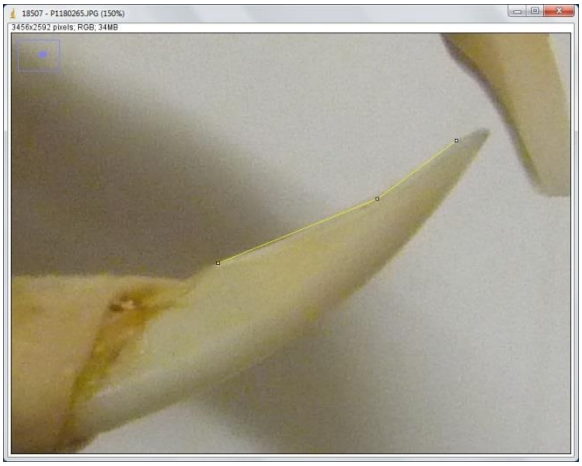
KU 14409 (*Aplodontia rufa*)

Upper Procumbency Angle



Upper Facet Angle

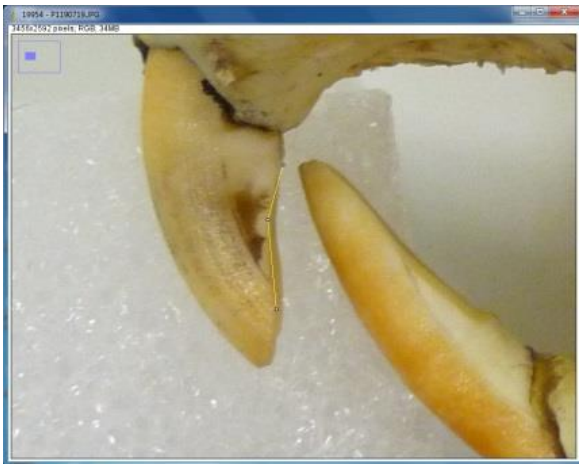
Lower Procumbency Angle



Lower Facet Angle

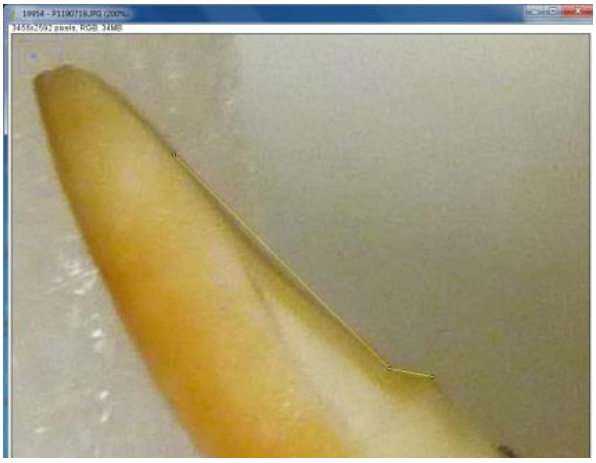
KU 18507 (*Cryptomys hottentotus*)

Upper Procumbency Angle



Upper Facet Angle

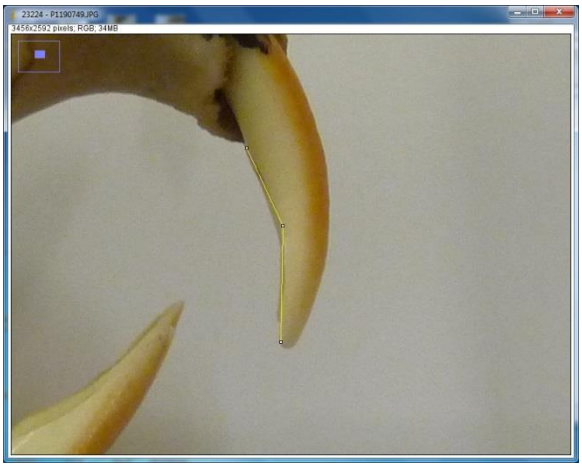
Lower Procumbency Angle



Lower Facet Angle

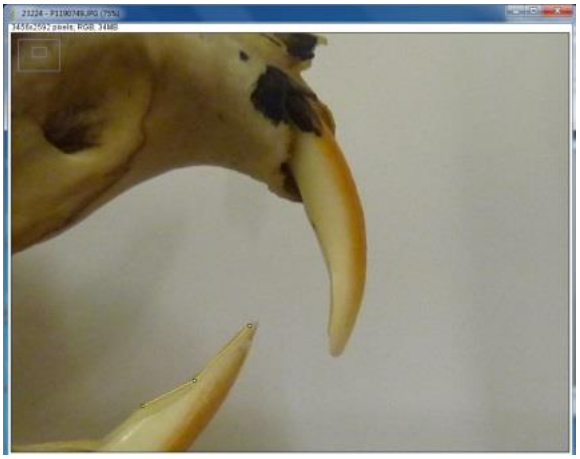
KU 19954 (*Marmota flaviventris*)

Upper Procumbency Angle



Upper Facet Angle

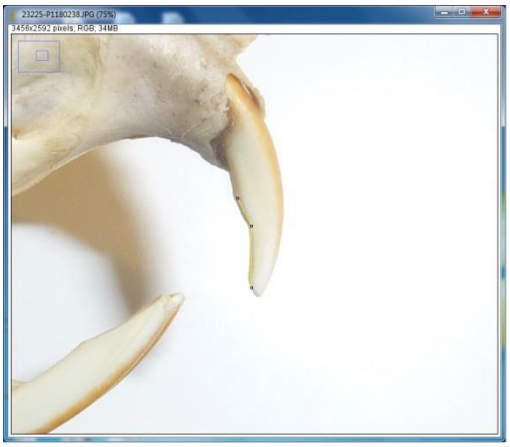
Lower Procumbency Angle



Lower Facet Angle

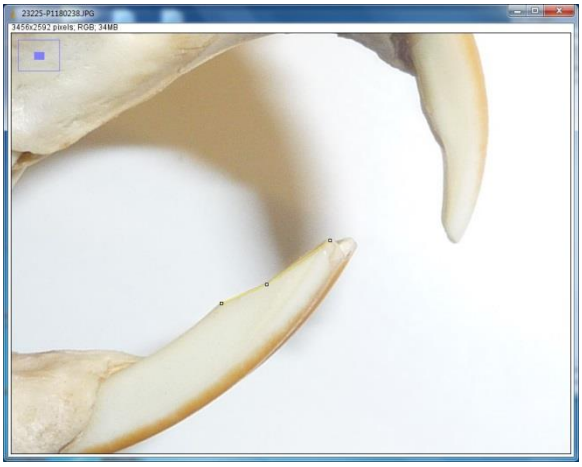
KU 23224 (*Thomomys bottae*)

Upper Procumbency Angle



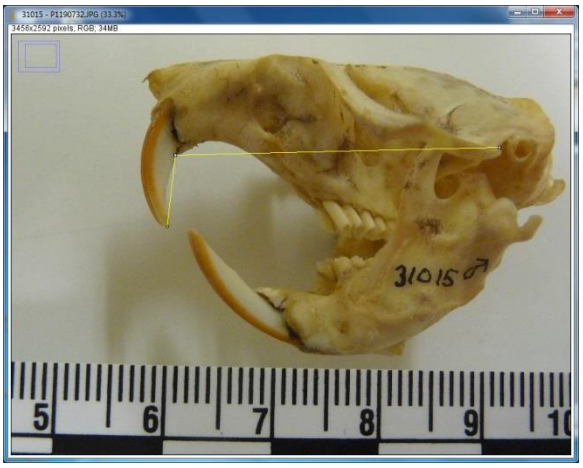
Upper Facet Angle

Lower Procumbency Angle

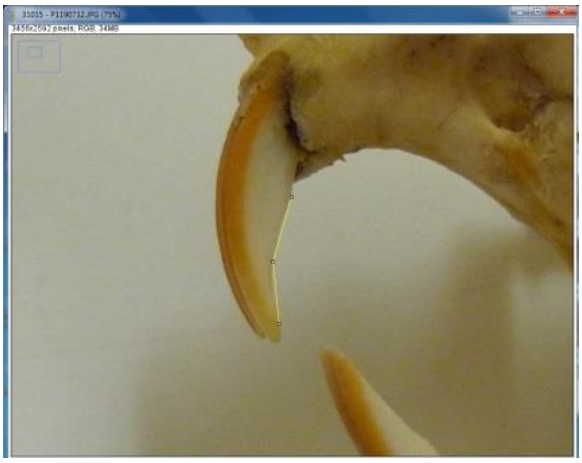


Lower Facet Angle

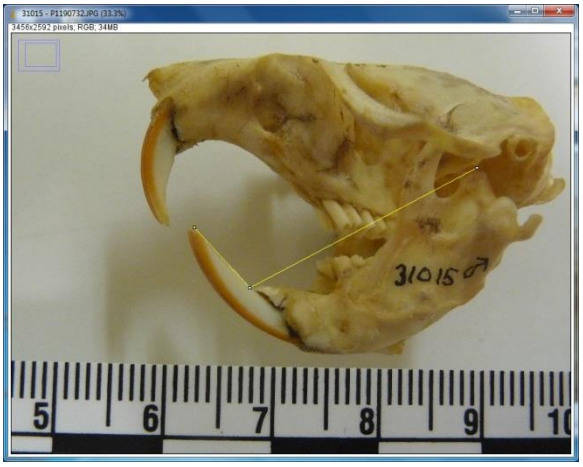
KU 23225 (*Thomomys bottae*)



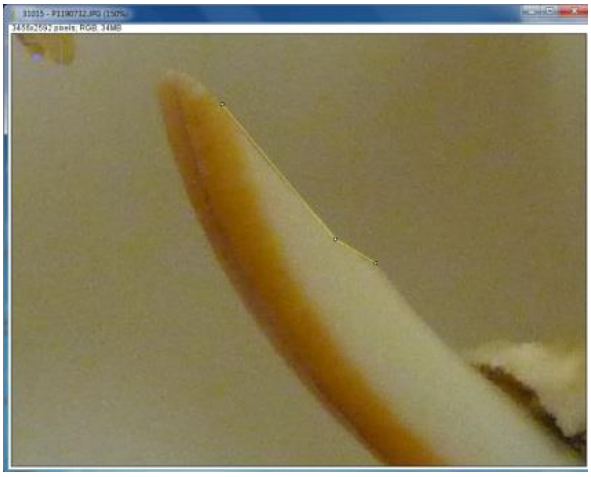
Upper Procumbency Angle



Upper Facet Angle



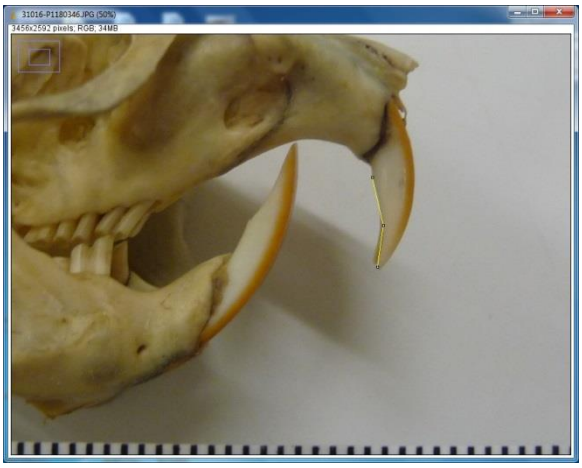
Lower Procumbency Angle



Lower Facet Angle

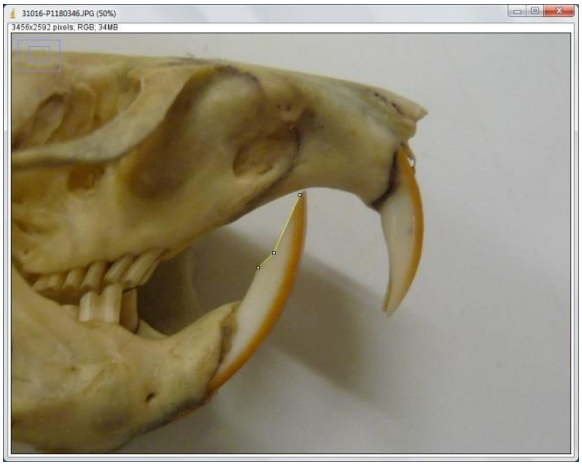
KU 31015 (*Pappogeomys bulleri*)

Upper Procumbency Angle



Upper Facet Angle

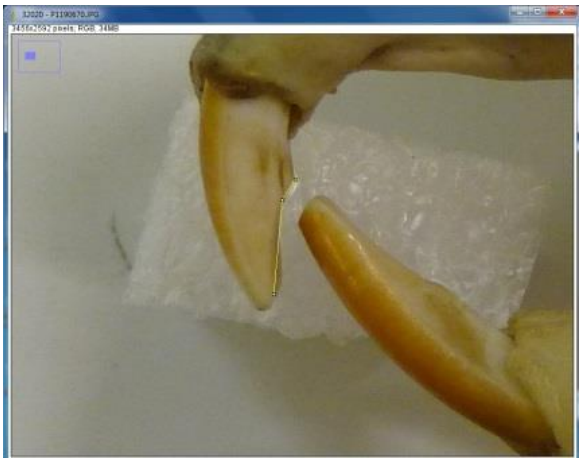
Lower Procumbency Angle



Lower Facet Angle

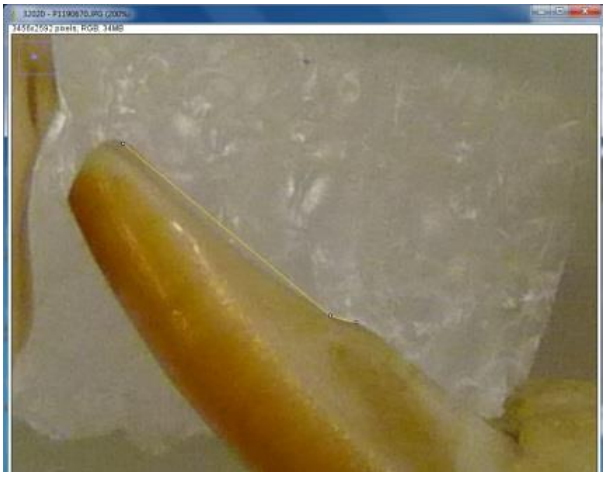
KU 31016 (*Pappogeomys bulleri*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle



Lower Facet Angle

KU 32020 (*Aplodontia rufa*)

Upper Procumbency Angle

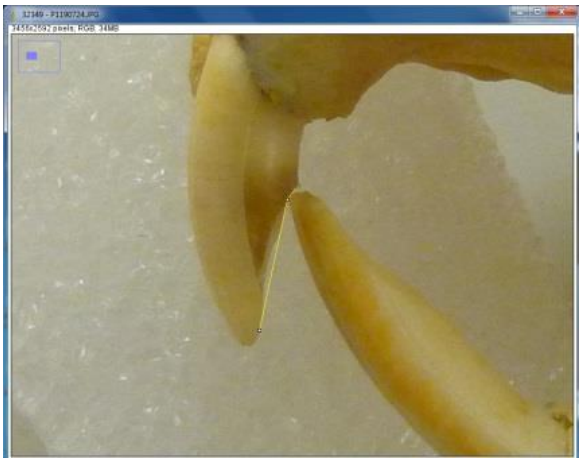
Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

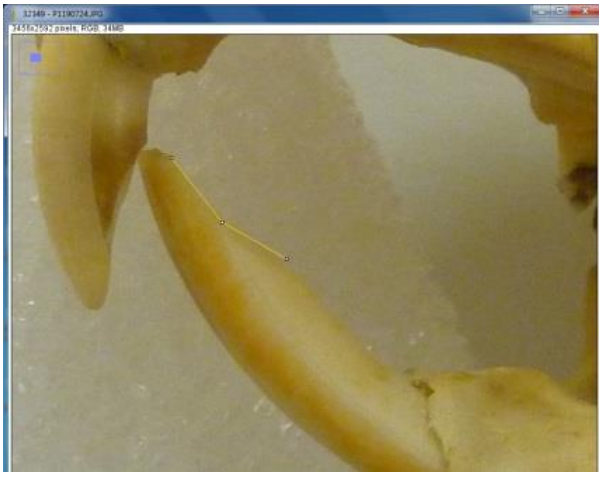
KU 32021 (*Aplodontia rufa*)

Upper Procumbency Angle



Upper Facet Angle

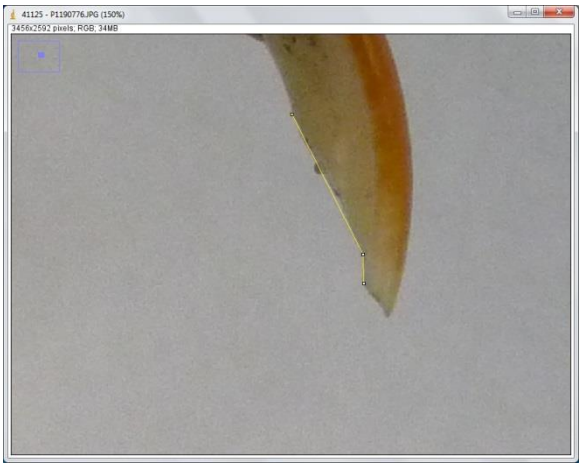
Lower Procumbency Angle



Lower Facet Angle

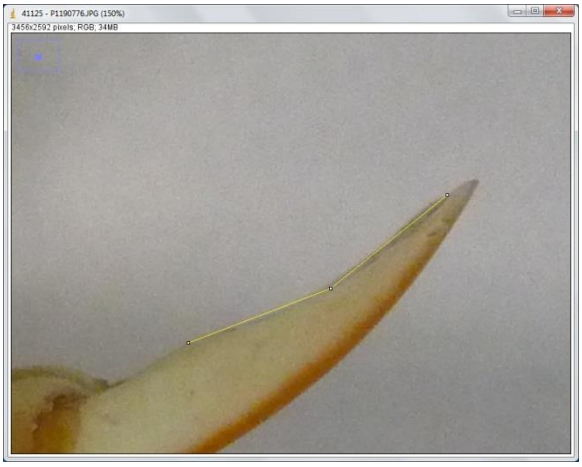
KU 32349 (*Marmota flaviventris*)

Upper Procumbency Angle



Upper Facet Angle

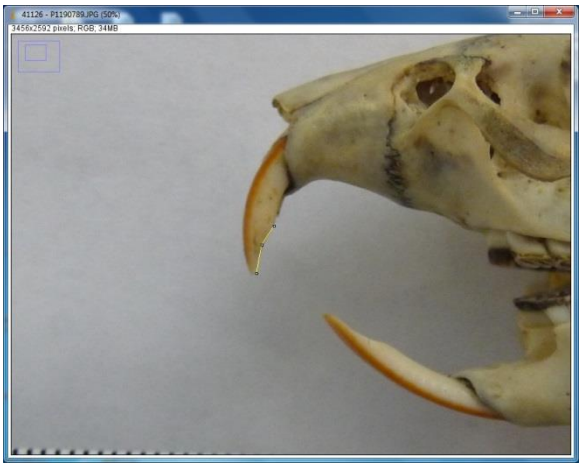
Lower Procumbency Angle



Lower Facet Angle

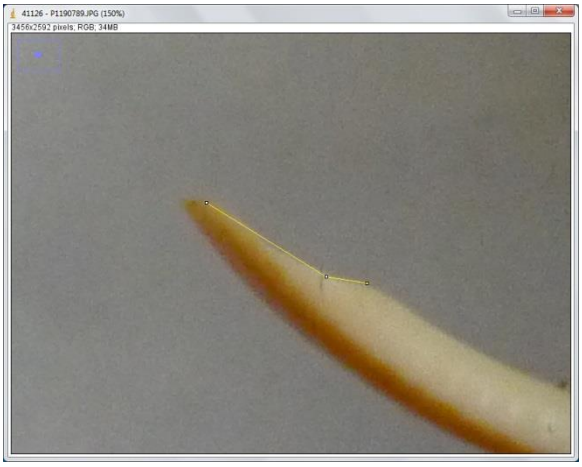
KU 41125 (*Tachyoryctes splendens*)

Upper Procumbency Angle



Upper Facet Angle

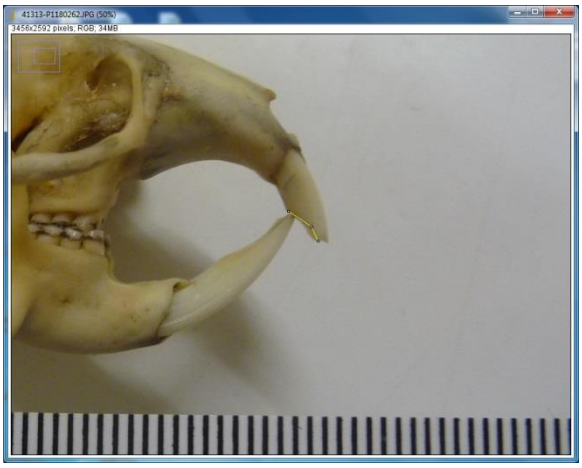
Lower Procumbency Angle



Lower Facet Angle

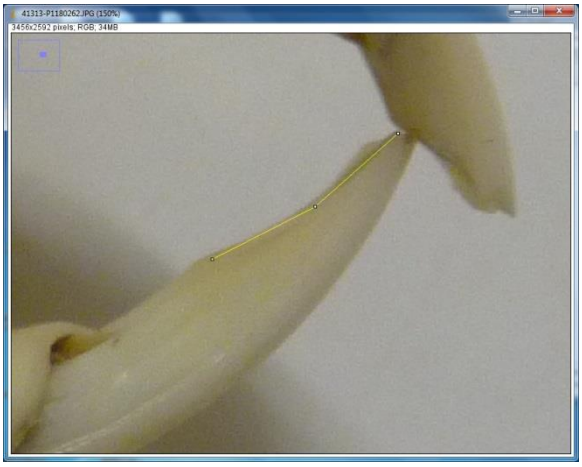
KU 41126 (*Tachyoryctes splendens*)

Upper Procumbency Angle



Upper Facet Angle

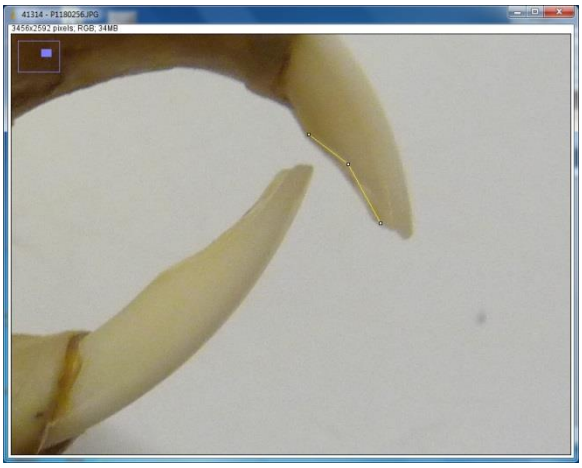
Lower Procumbency Angle



Lower Facet Angle

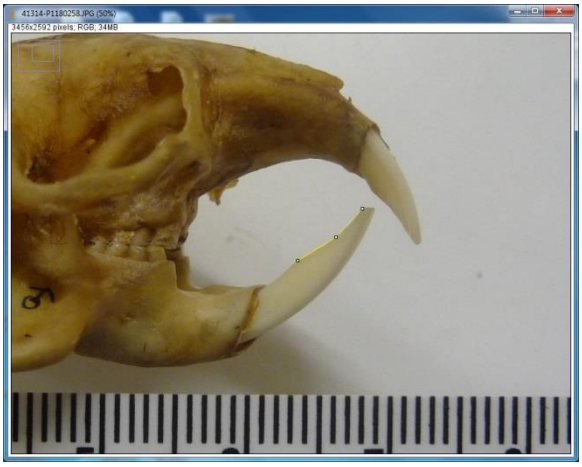
KU 41313 (*Cryptomys hottentotus*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle



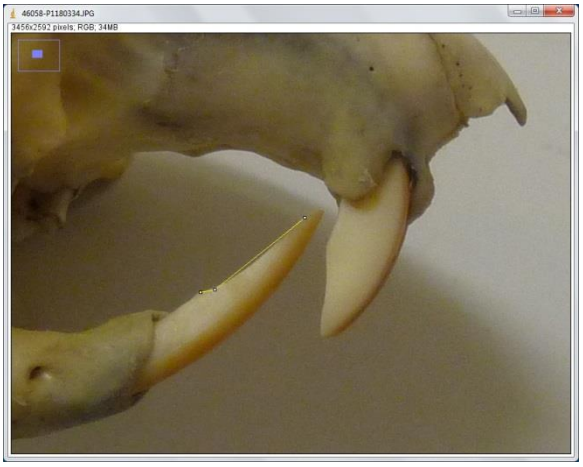
Lower Facet Angle

KU 41314 (*Cryptomys hottentotus*)

Upper Procumbency Angle

Upper Facet Angle

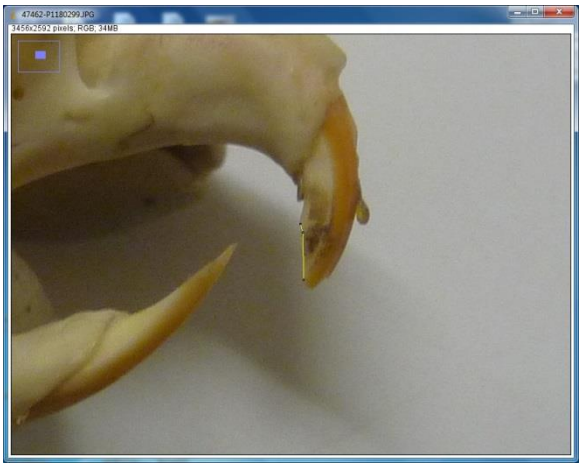
Lower Procumbency Angle



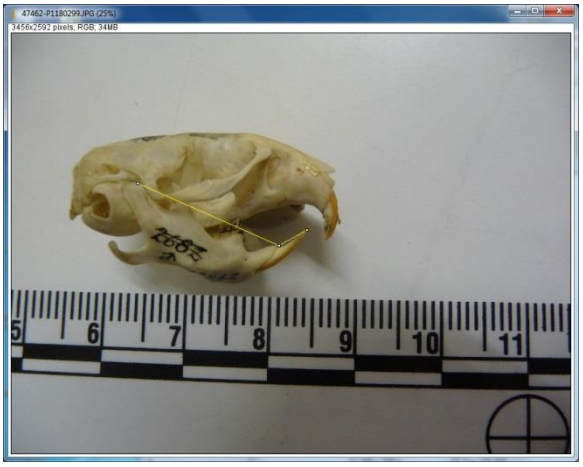
Lower Facet Angle

KU 46058 (*Citellus tridecemlineatus*)

Upper Procumbency Angle



Upper Facet Angle



Lower Procumbency Angle

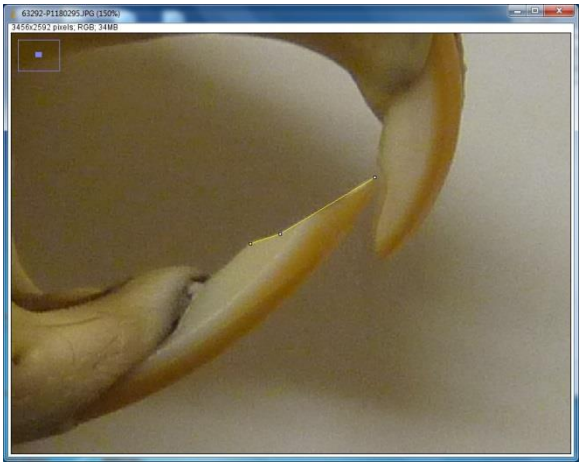
Lower Facet Angle

KU 47462 (Microtus californius)

Upper Procumbency Angle

Upper Facet Angle

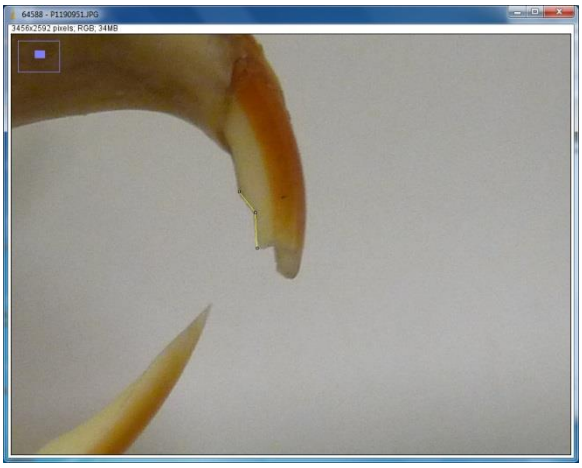
Lower Procumbency Angle



Lower Facet Angle

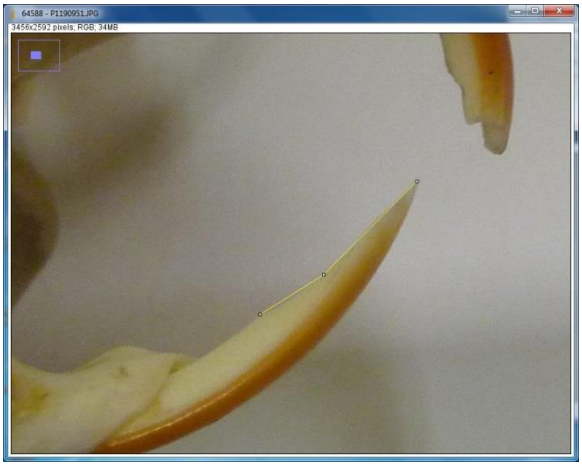
KU 63292 (*Microtus californicus*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle



Lower Facet Angle

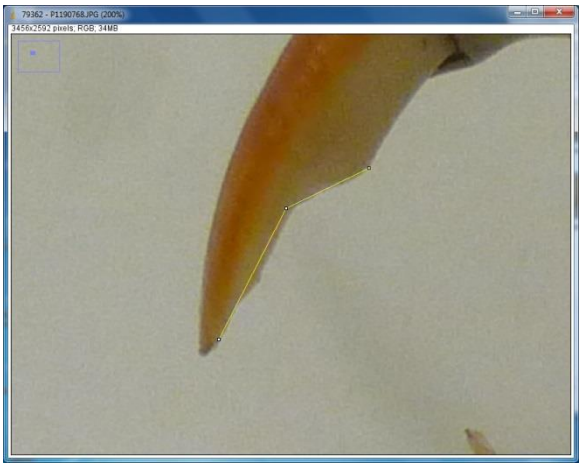
KU 64588 (*Arvicola terrestris*)

Upper Procumbency Angle

Upper Facet Angle

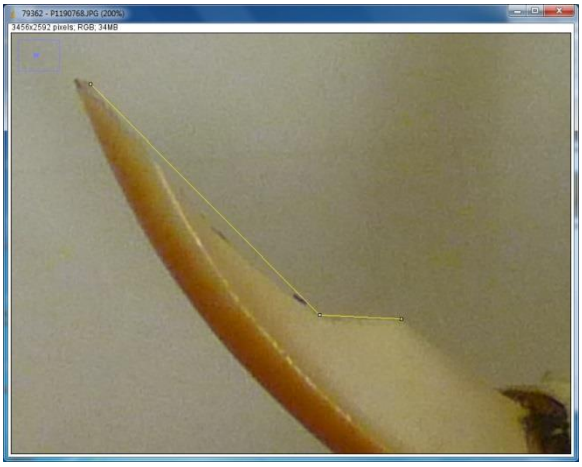
KU 79361 (*Rhizomys pruinosus*)

Upper Procumbency Angle



Upper Facet Angle

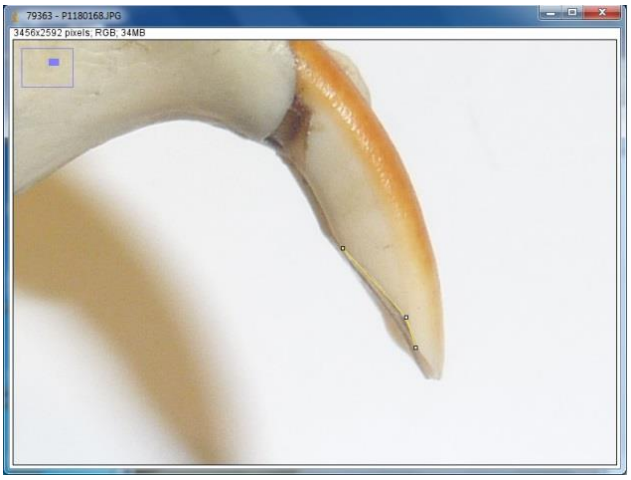
Lower Procumbency Angle



Lower Facet Angle

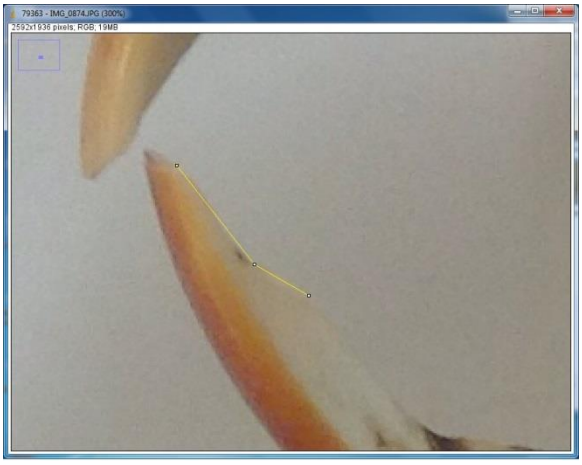
KU 79362 (*Cannomys badius*)

Upper Procumbency Angle



Upper Facet Angle

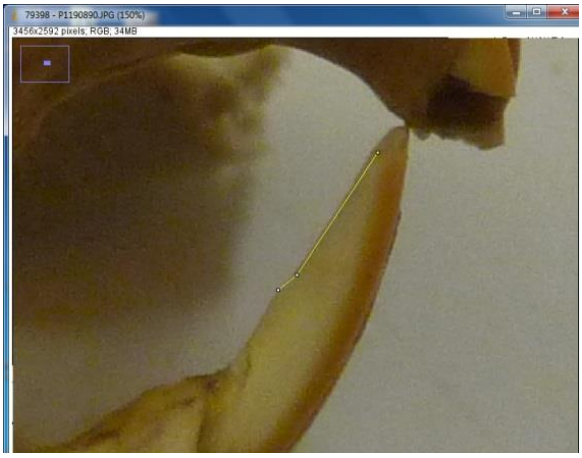
Lower Procumbency Angle



Lower Facet Angle

KU 79363 (*Cannomys badius*)

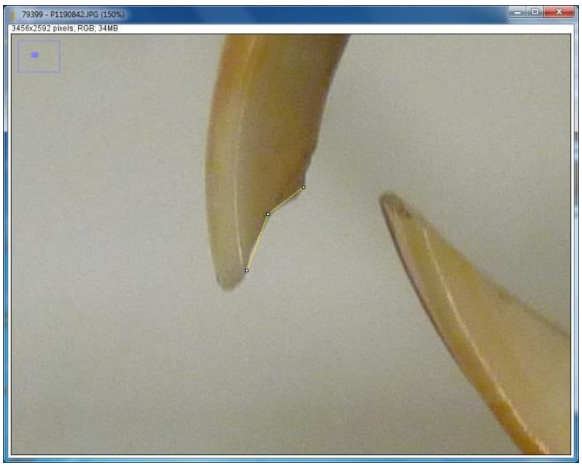
Lower Procumbency Angle



Lower Facet Angle

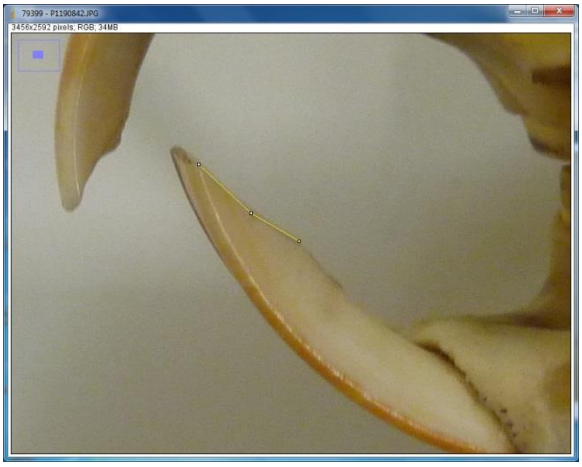
KU 79398 (*Aconaemys fuscus*)

Upper Procumbency Angle



Upper Facet Angle

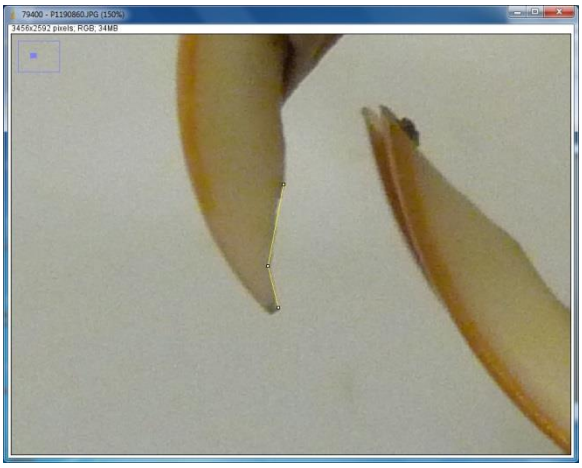
Lower Procumbency Angle



Lower Facet Angle

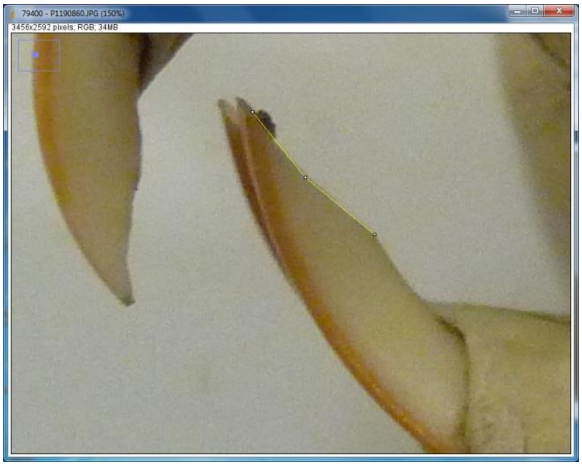
KU 79399 (*Ctenomys lewisi*)

Upper Procumbency Angle



Upper Facet Angle

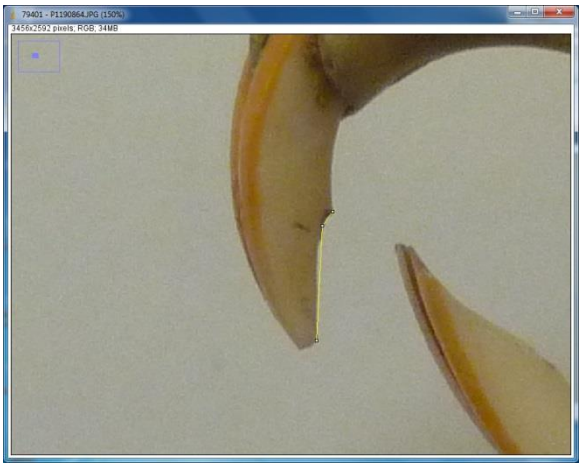
Lower Procumbency Angle



Lower Facet Angle

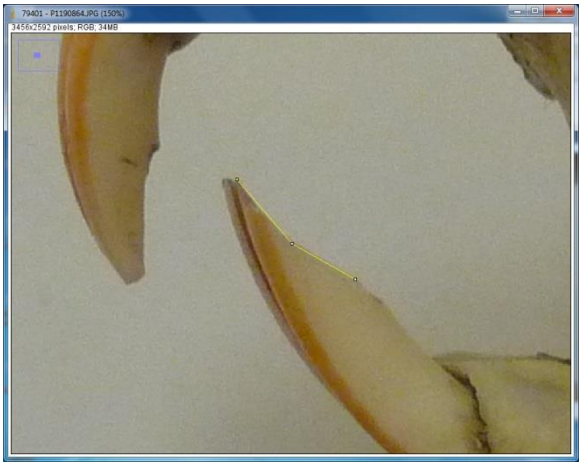
KU 79400 (*Ctenomys mendocinus*)

Upper Procumbency Angle



Upper Facet Angle

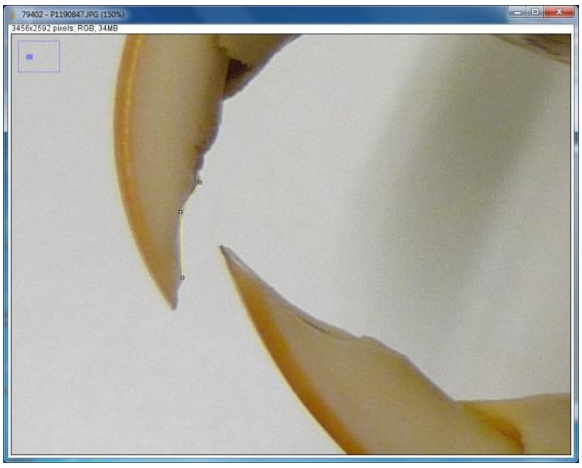
Lower Procumbency Angle



Lower Facet Angle

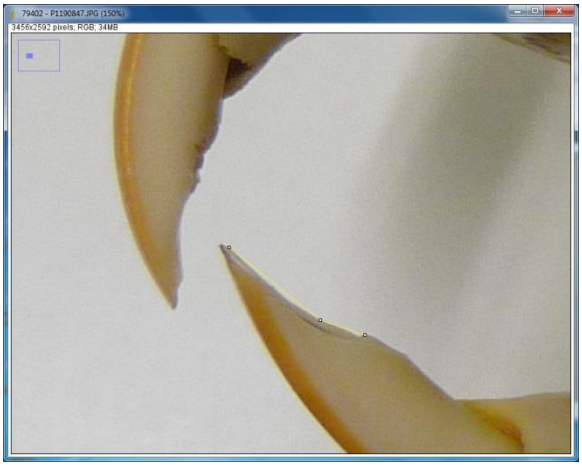
KU 79401 (*Ctenomys mendocinus*)

Upper Procumbency Angle



Upper Facet Angle

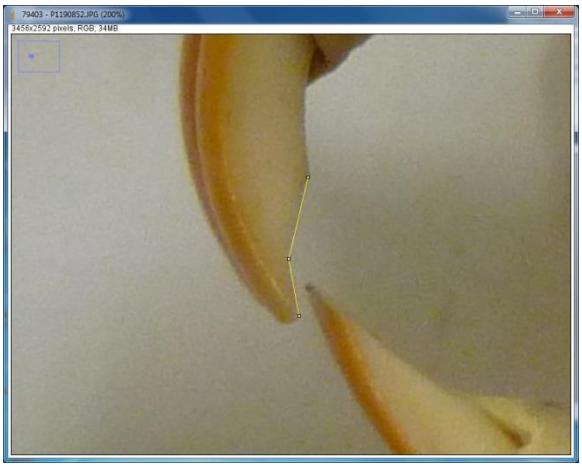
Lower Procumbency Angle



Lower Facet Angle

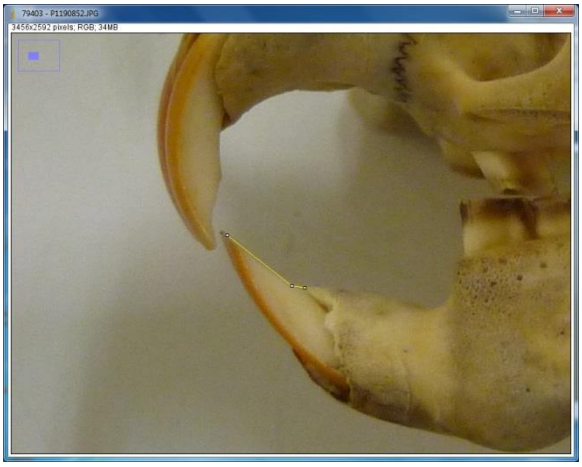
KU 79402 (*Ctenomys sylvanus*)

Upper Procumbency Angle



Upper Facet Angle

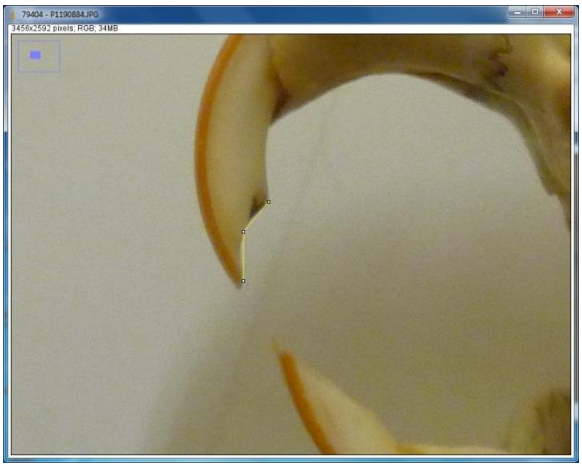
Lower Procumbency Angle



Lower Facet Angle

KU 79403 (*Ctenomys frater*)

Upper Procumbency Angle



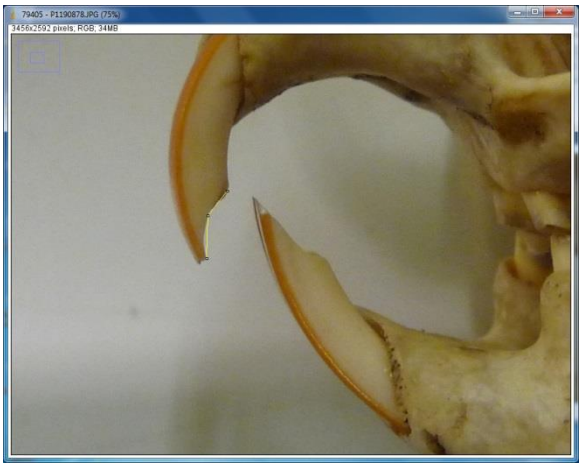
Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

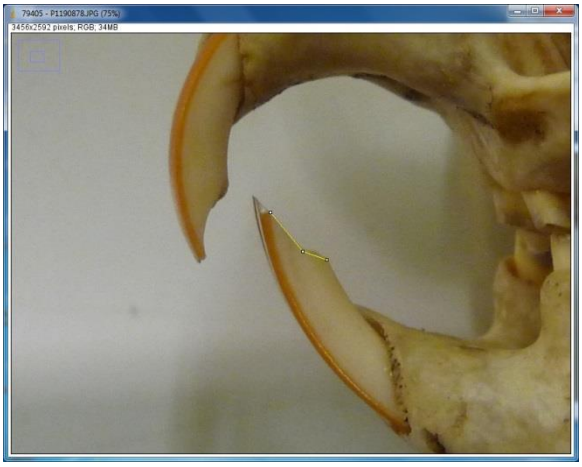
KU 79404 (*Ctenomys rionegrensis*)

Upper Procumbency Angle



Upper Facet Angle

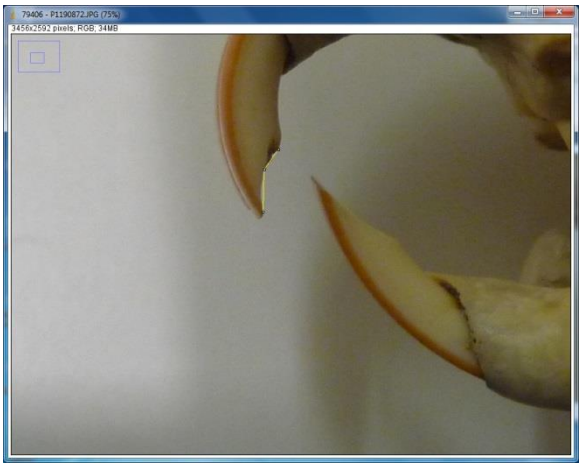
Lower Procumbency Angle



Lower Facet Angle

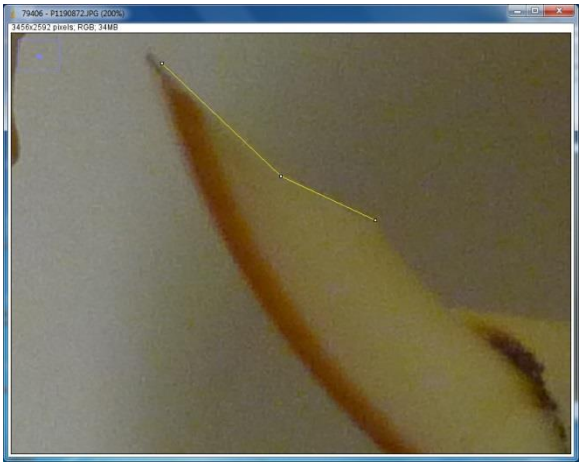
KU 79405 (*Ctenomys rionegrensis*)

Upper Procumbency Angle



Upper Facet Angle

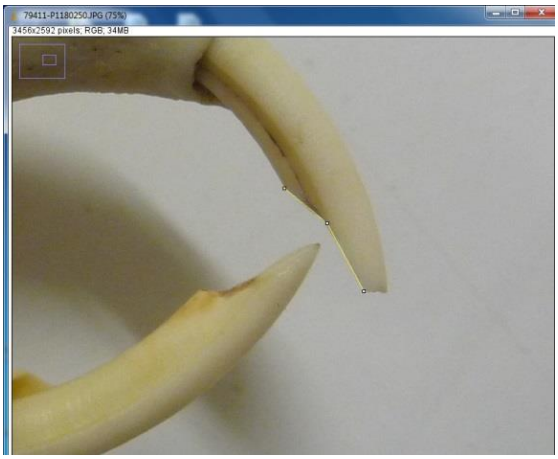
Lower Procumbency Angle



Lower Facet Angle

KU 79406 (*Ctenomys rionegrensis*)

Upper Procumbency Angle



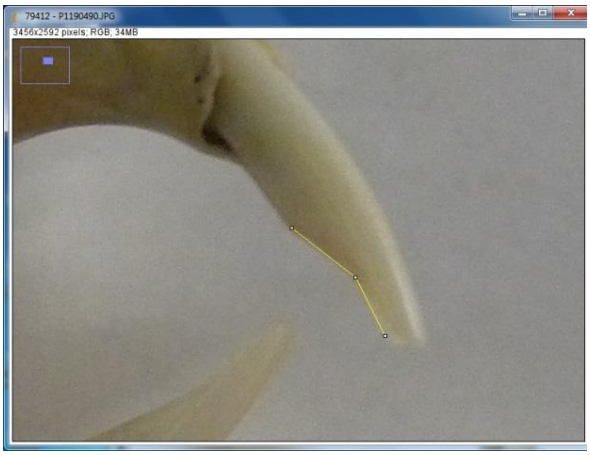
Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

KU 79411 (*Cryptomys hottentotus*)

Upper Procumbency Angle



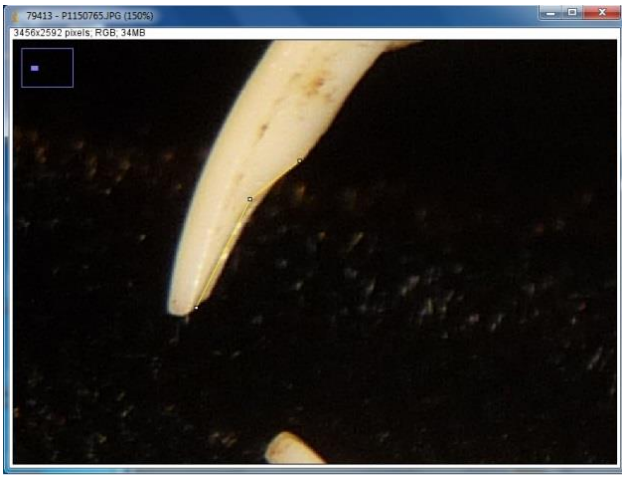
Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

KU 79412 (*Heliophobius argenteocinereus*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle

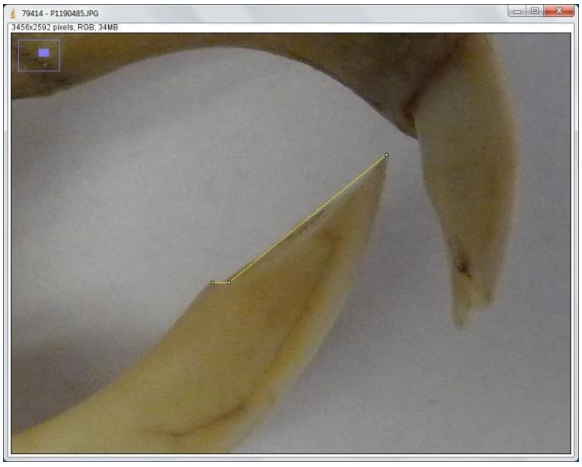
Lower Facet Angle

KU 79413 (*Heliophobius argenteocinereus*)

Upper Procumbency Angle

Upper Facet Angle

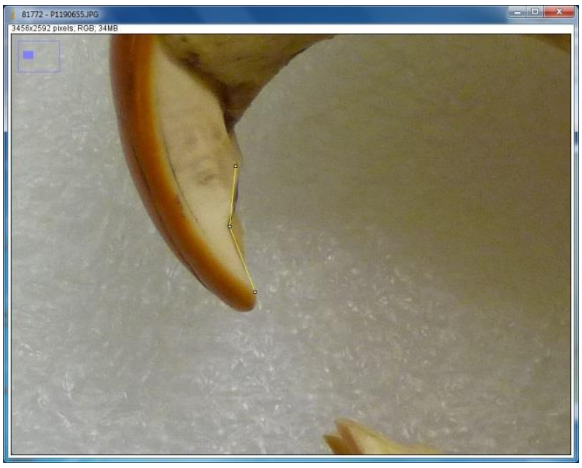
Lower Procumbency Angle



Lower Facet Angle

KU 79414 (*Bathyergus suillus*)

Upper Procumbency Angle



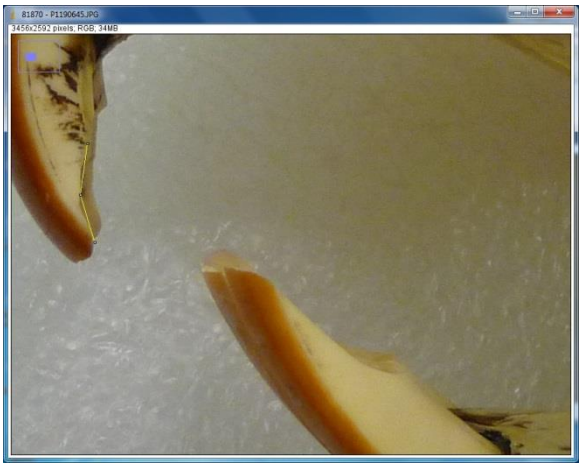
Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

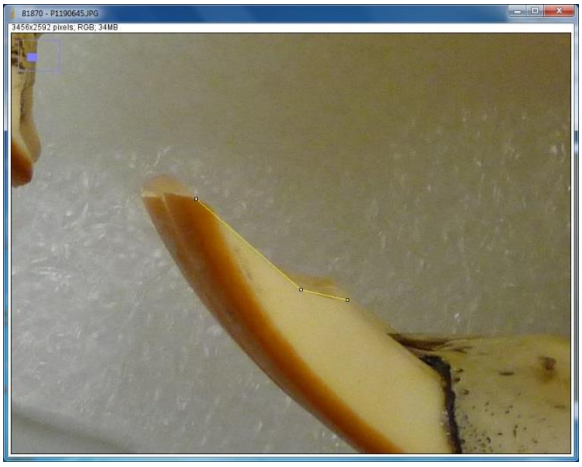
KU 81772 (*Castor canadensis*)

Upper Procumbency Angle



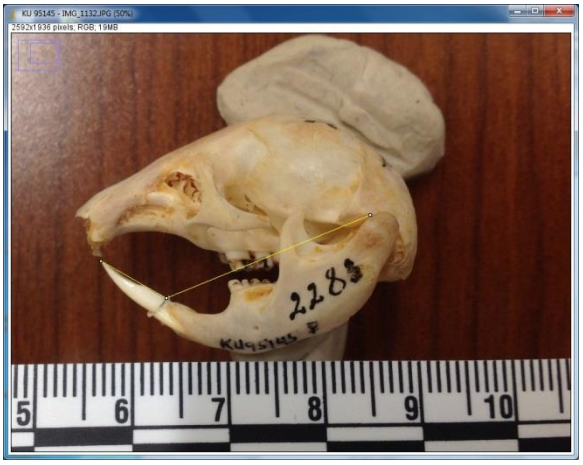
Upper Facet Angle

Lower Procumbency Angle

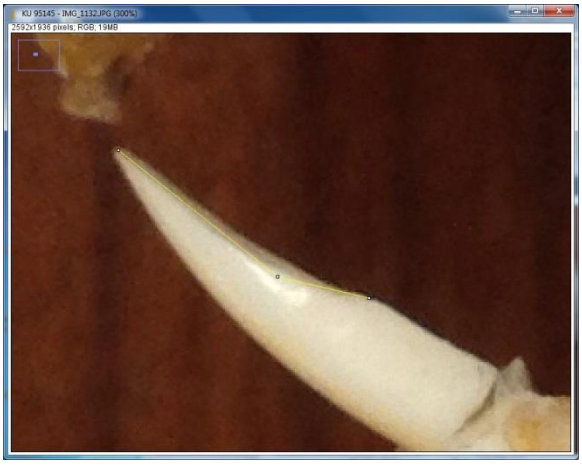


Lower Facet Angle

KU 81870 (*Castor canadensis*)



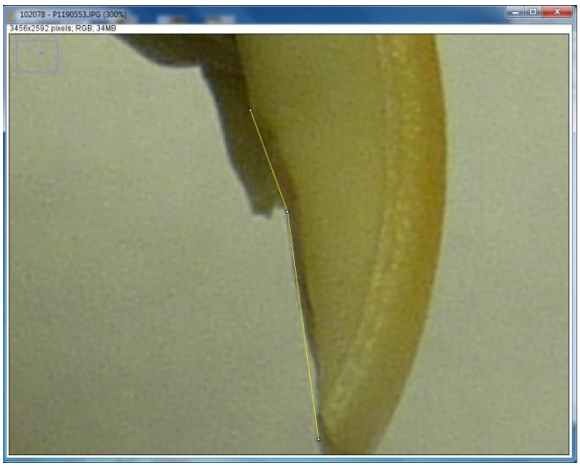
Lower Procumbency Angle



Lower Facet Angle

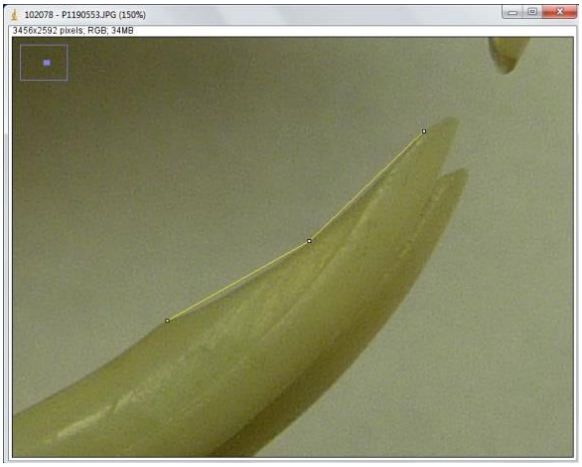
KU 95145 (*Spalax microphthalmus*)

Upper Procumbency Angle



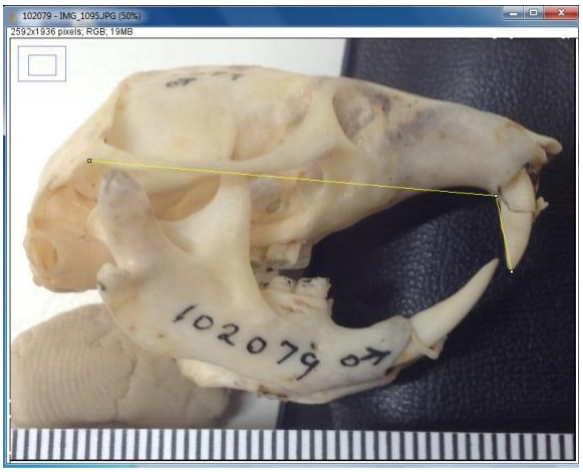
Upper Facet Angle

Lower Procumbency Angle

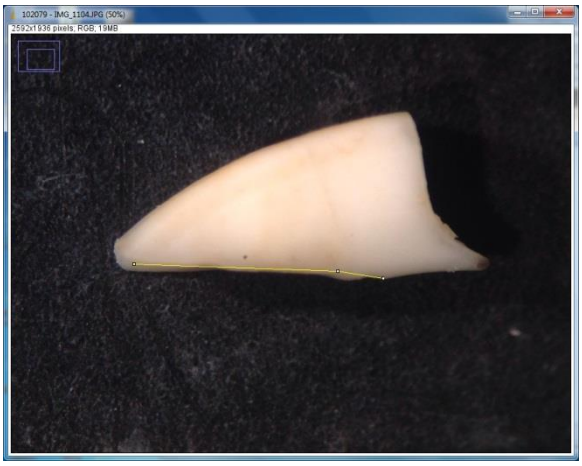


Lower Facet Angle

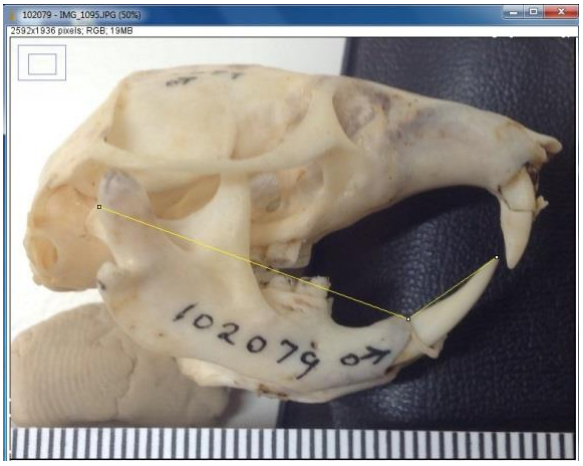
KU 102078 (*Nannospalax leucodon*)



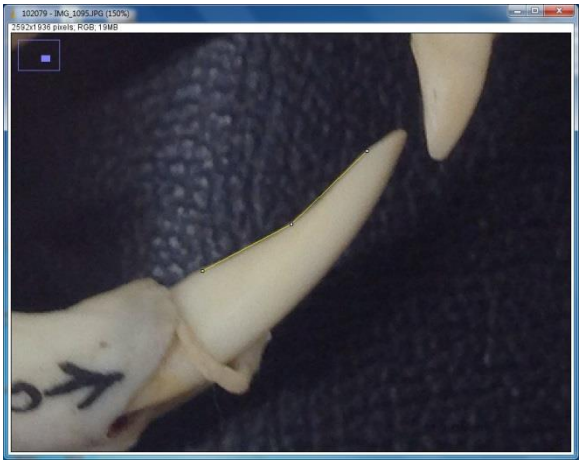
Upper Procumbency Angle



Upper Facet Angle



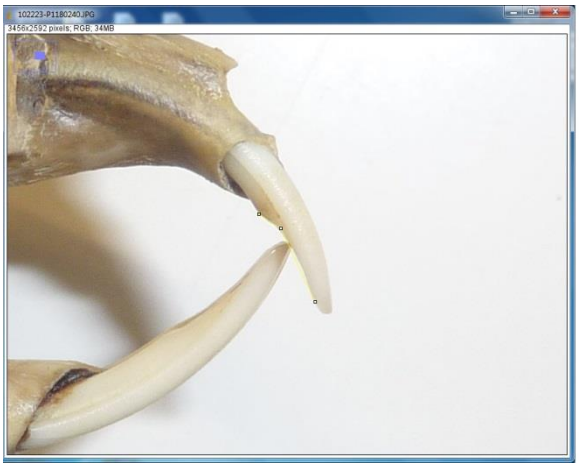
Lower Procumbency Angle



Lower Facet Angle

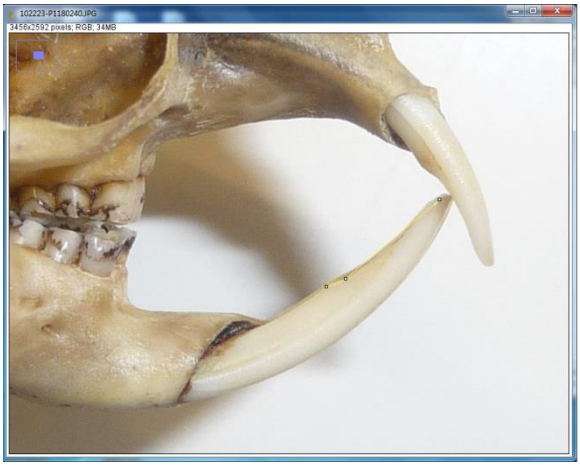
KU 102079 (*Nannospalax leucodon*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle



Lower Facet Angle

KU 102223 (*Cryptomys hottentotus*)

Upper Procumbency Angle

Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

KU 116695 (*Cratogeomys castanops*)

Upper Procumbency Angle

Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

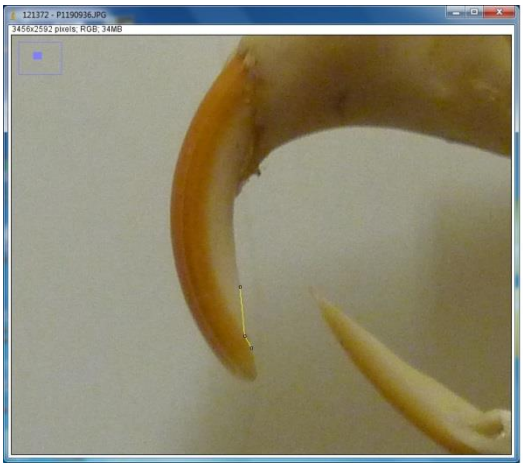
KU 116697 (*Cratogeomys castanops*)

Upper Procumbency Angle

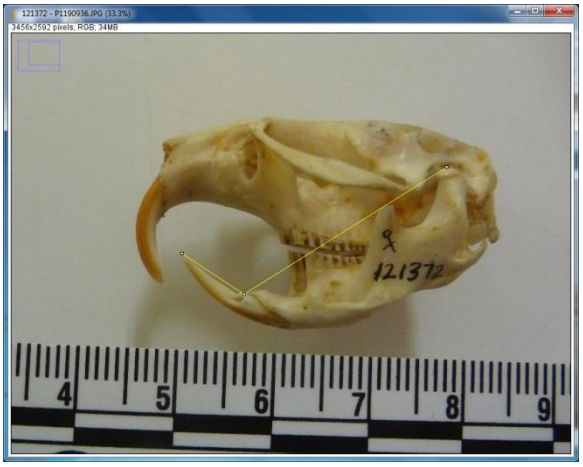
Upper Facet Angle

KU 117054 (*Arvicola terrestris*)

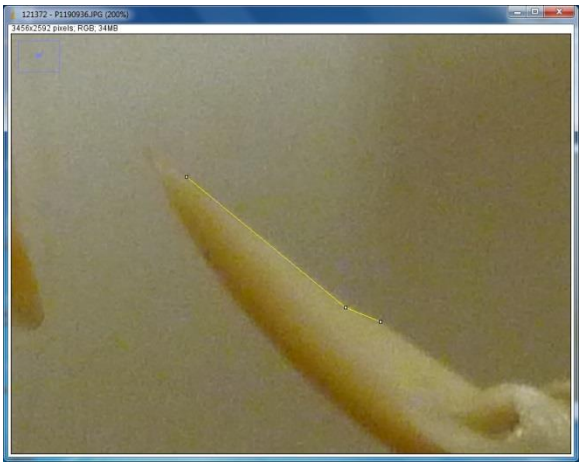
Upper Procumbency Angle



Upper Facet Angle



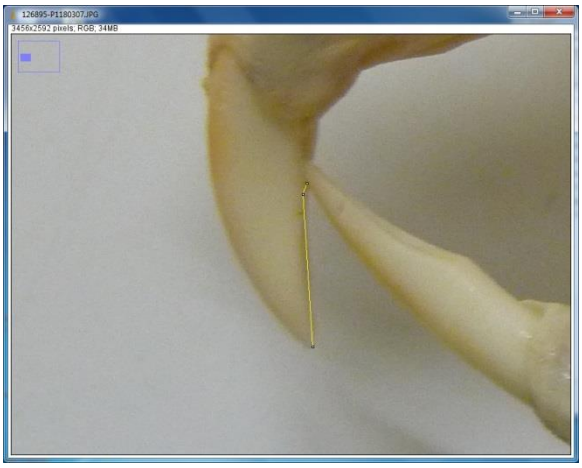
Lower Procumbency Angle



Lower Facet Angle

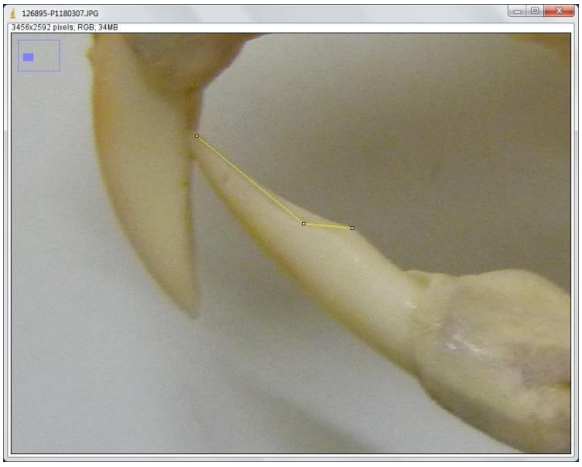
KU 121372 (*Arvicola terrestris*)

Upper Procumbency Angle



Upper Facet Angle

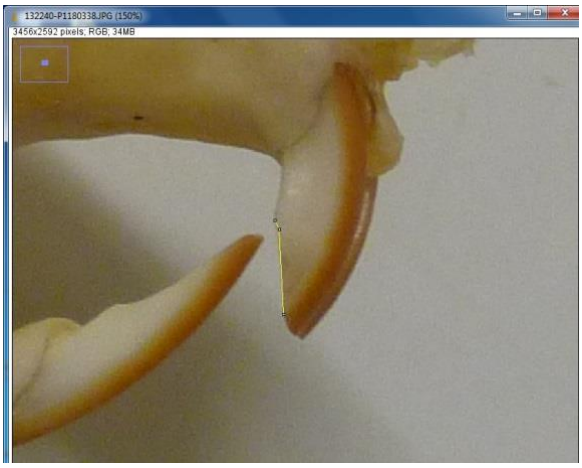
Lower Procumbency Angle



Lower Facet Angle

KU 126895 (*Cynomys gunnisoni*)

Upper Procumbency Angle



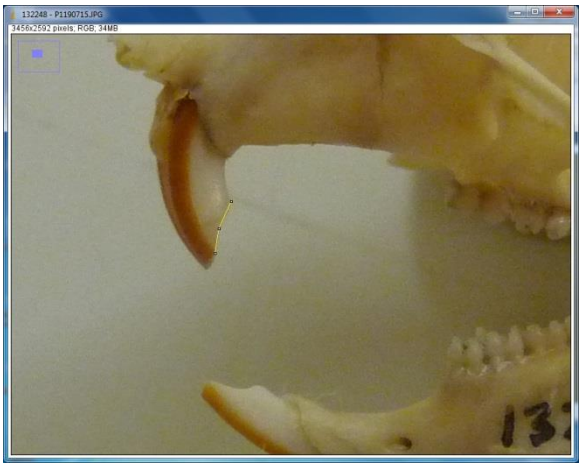
Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

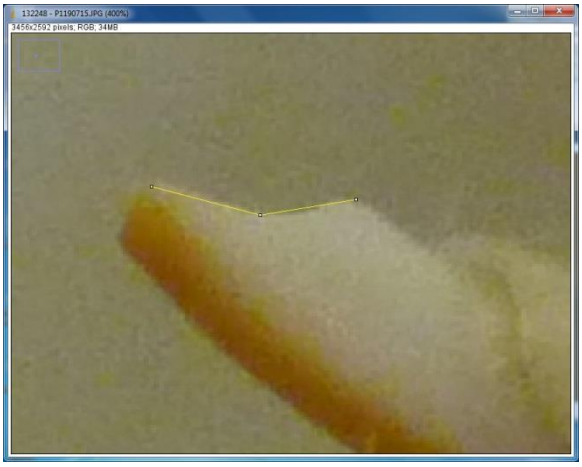
KU 132240 (*Tamias palmeri*)

Upper Procumbency Angle



Upper Facet Angle

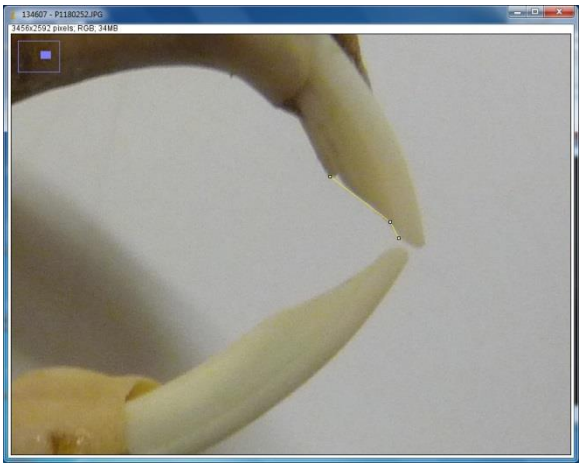
Lower Procumbency Angle



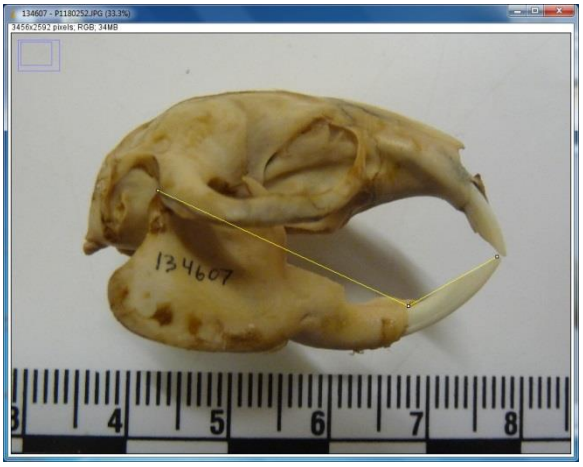
Lower Facet Angle

KU 132248 (*Tamias palmeri*)

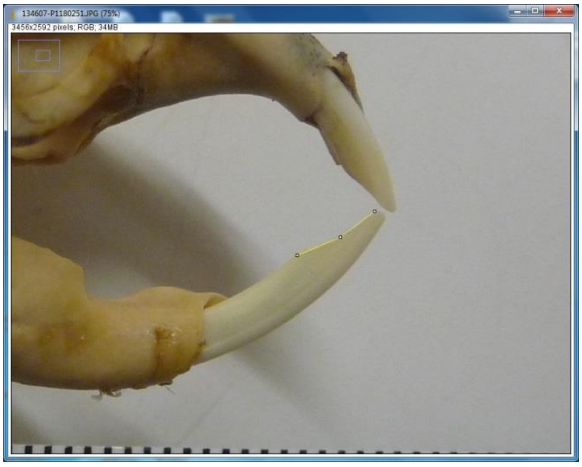
Upper Procumbency Angle



Upper Facet Angle

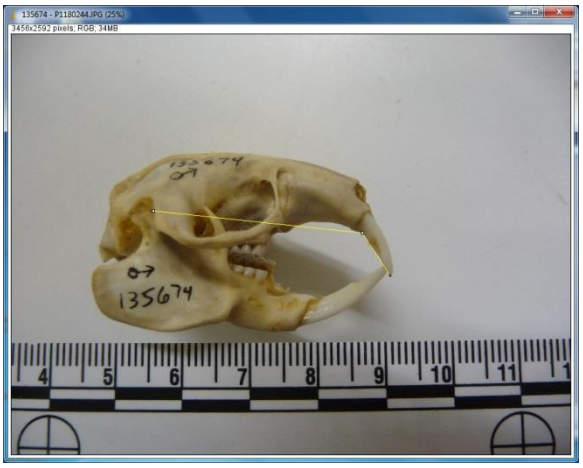


Lower Procumbency Angle

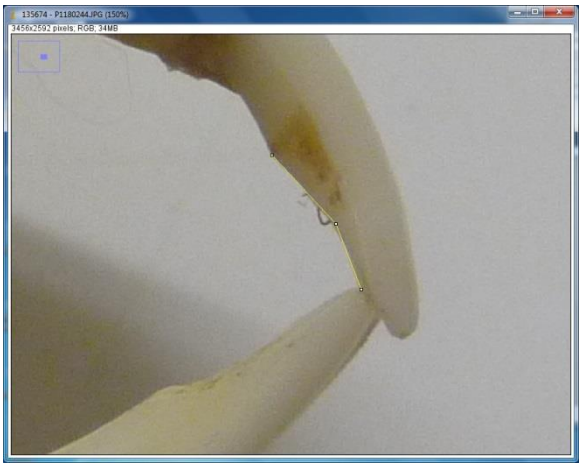


Lower Facet Angle

KU 134607 (*Cryptomys hottentotus*)



Upper Procumbency Angle



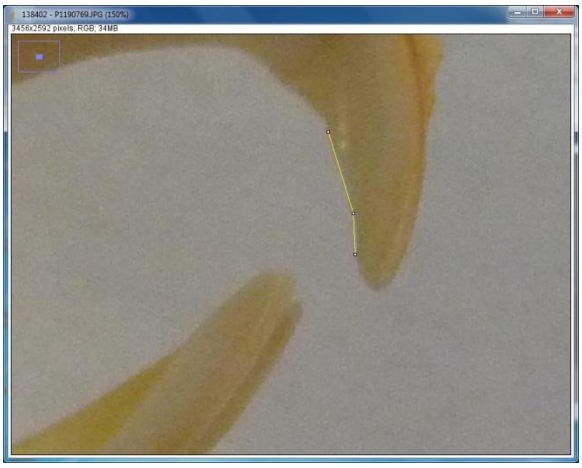
Upper Facet Angle

Lower Procumbency Angle

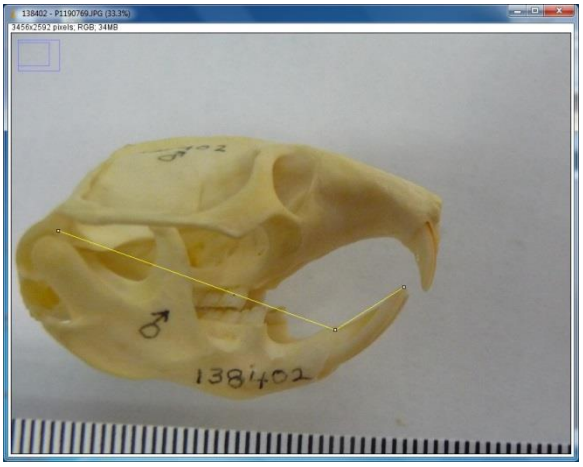
Lower Facet Angle

KU 135674 (*Cryptomys hottentotus*)

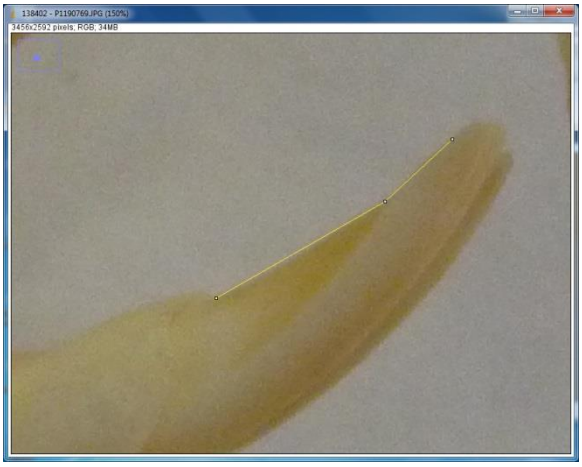
Upper Procumbency Angle



Upper Facet Angle



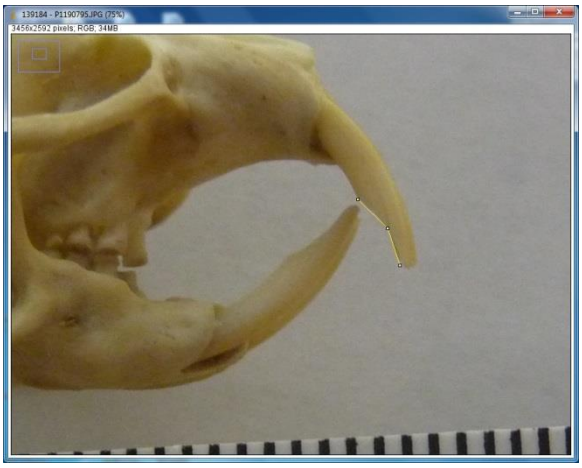
Lower Procumbency Angle



Lower Facet Angle

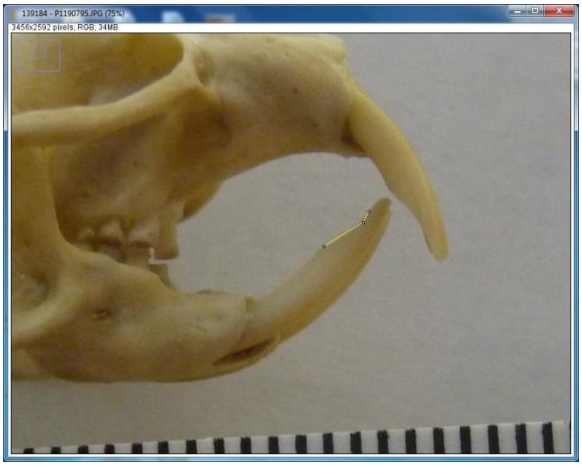
KU 138402 (*Nannospalax leucodon*)

Upper Procumbency Angle



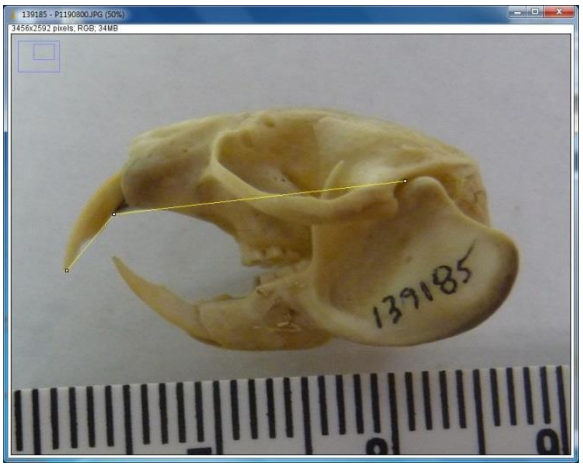
Upper Facet Angle

Lower Procumbency Angle

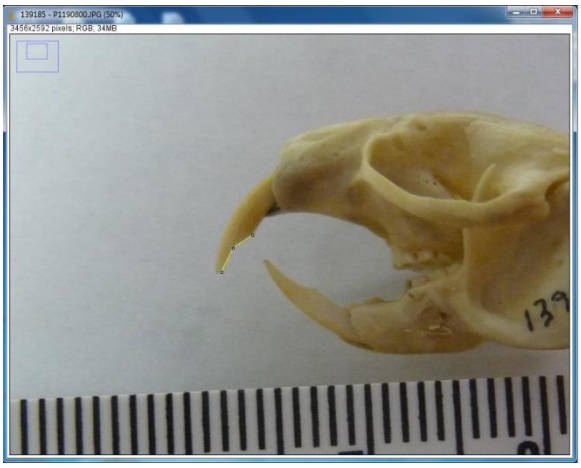


Lower Facet Angle

KU 139184 (*Heterocephalus glaber*)

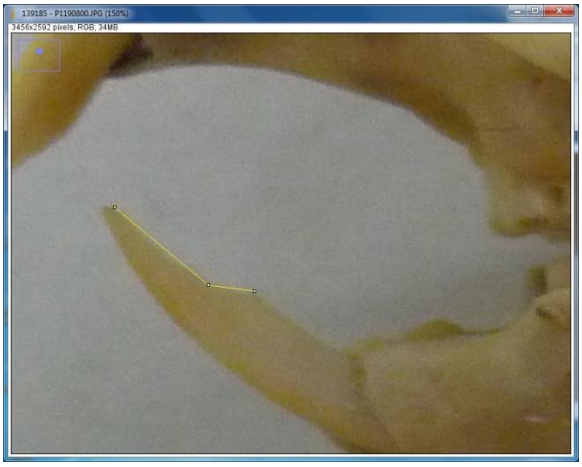


Upper Procumbency Angle



Upper Facet Angle

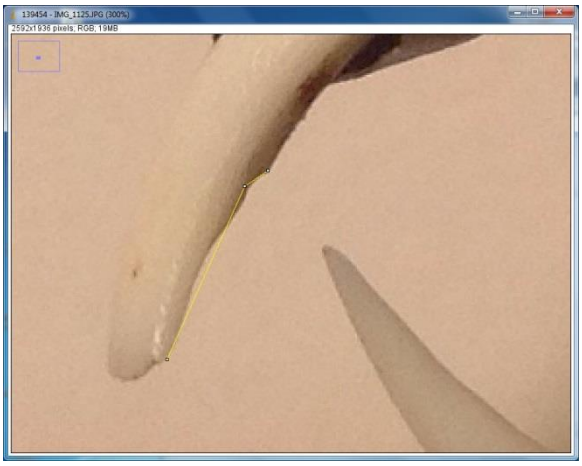
Lower Procumbency Angle



Lower Facet Angle

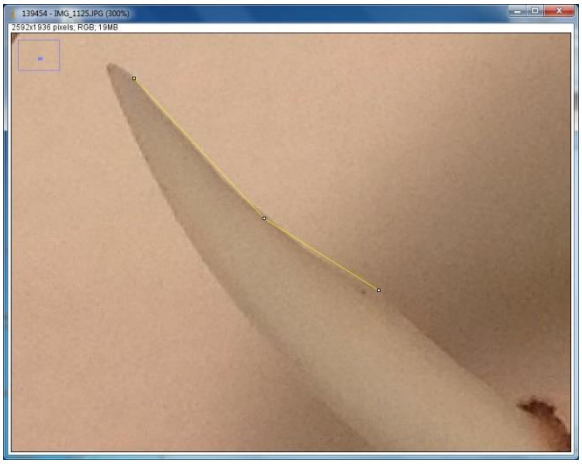
KU 139185 (*Heterocephalus glaber*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle



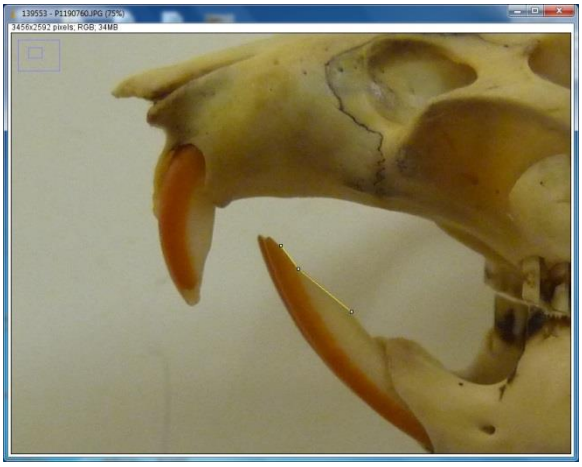
Lower Facet Angle

KU 139454 (*Ellobius talpinus*)

Upper Procumbency Angle

Upper Facet Angle

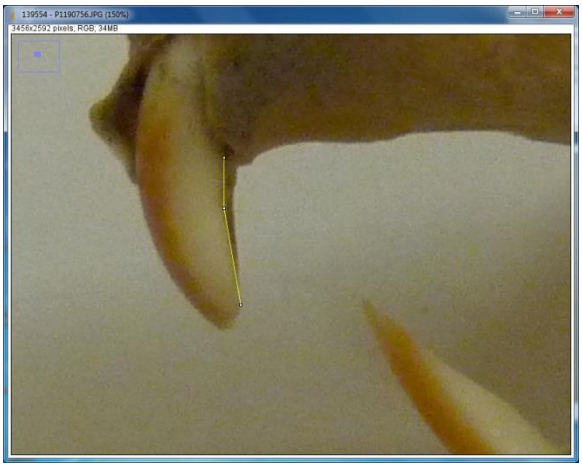
Lower Procumbency Angle



Lower Facet Angle

KU 139553 (*Eospalax fontanieri*)

Upper Procumbency Angle

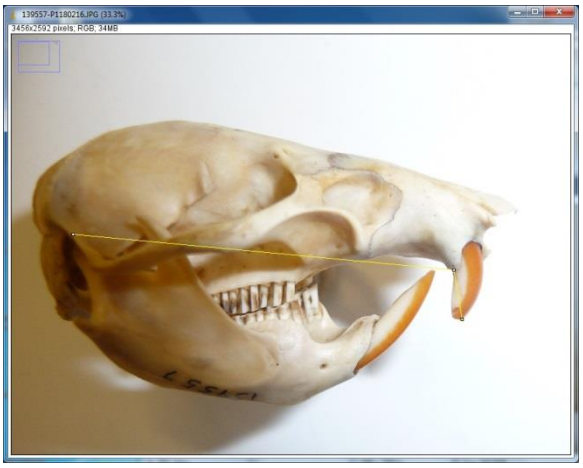


Upper Facet Angle

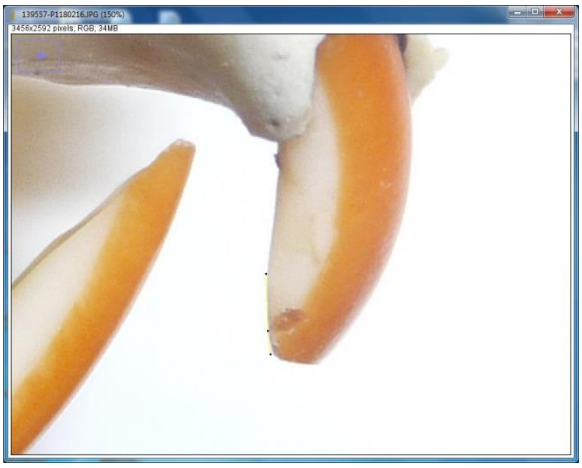
Lower Procumbency Angle

Lower Facet Angle

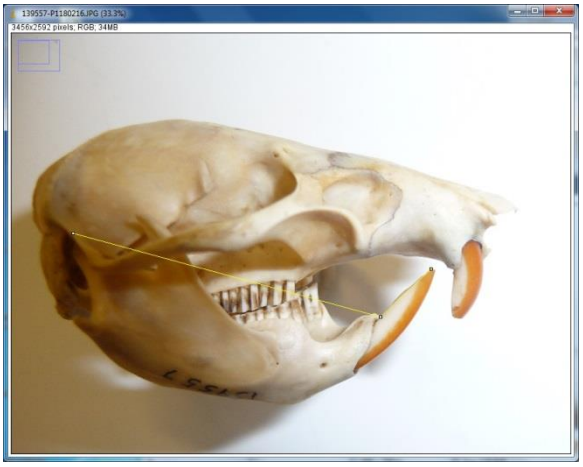
KU 139554 (*Myospalax baileyi*)



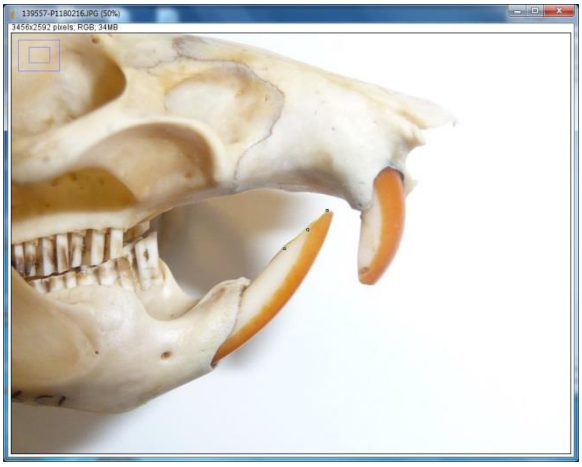
Upper Procumbency Angle



Upper Facet Angle



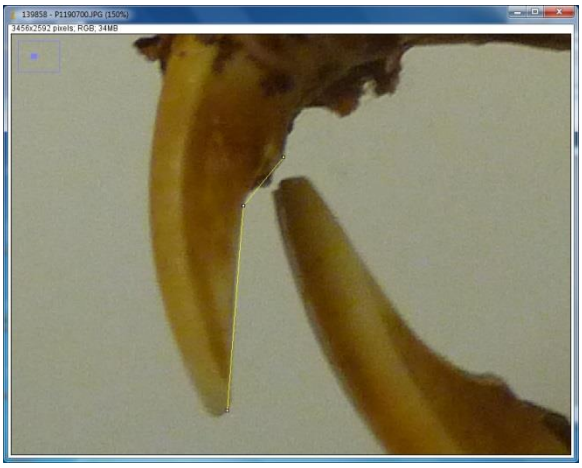
Lower Procumbency Angle



Lower Facet Angle

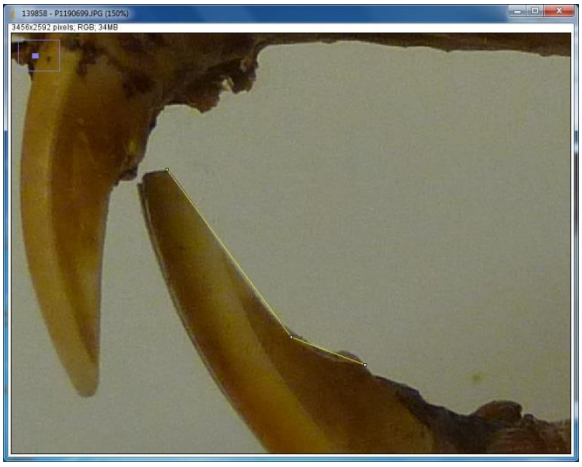
KU 139557 (*Myospalax baileyi*)

Upper Procumbency Angle



Upper Facet Angle

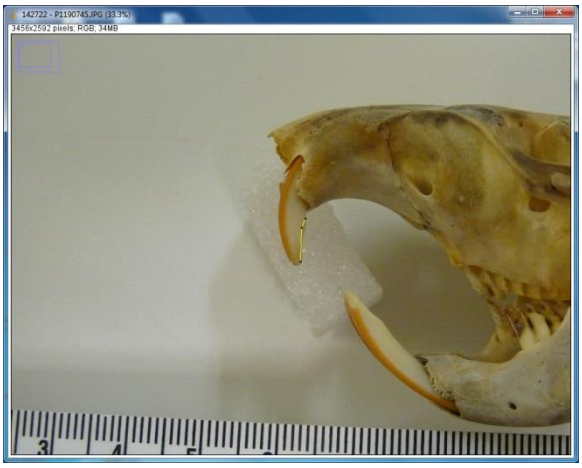
Lower Procumbency Angle



Lower Facet Angle

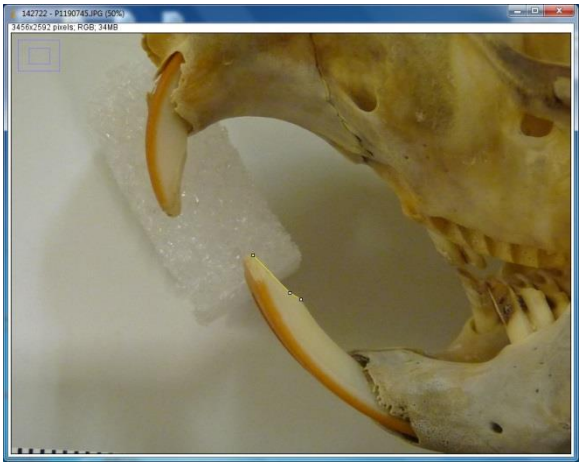
KU 139858 (*Aplodontia rufa*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle



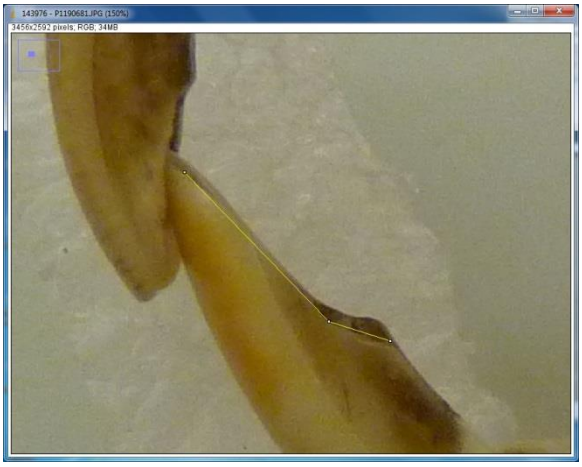
Lower Facet Angle

KU 142722 (*Orthogeomys heterodus*)

Upper Procumbency Angle

Upper Facet Angle

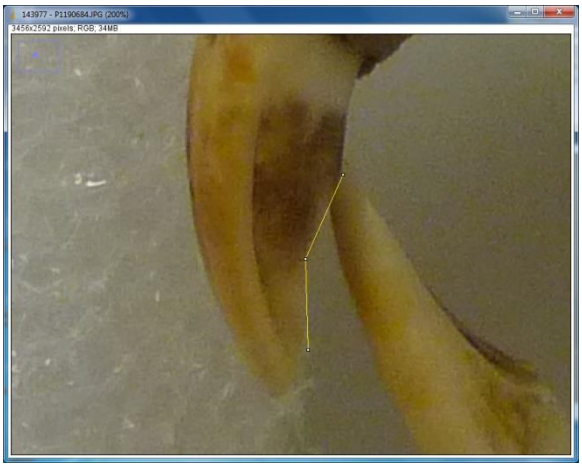
Lower Procumbency Angle



Lower Facet Angle

KU 143976 (*Aplodontia rufa*)

Upper Procumbency Angle



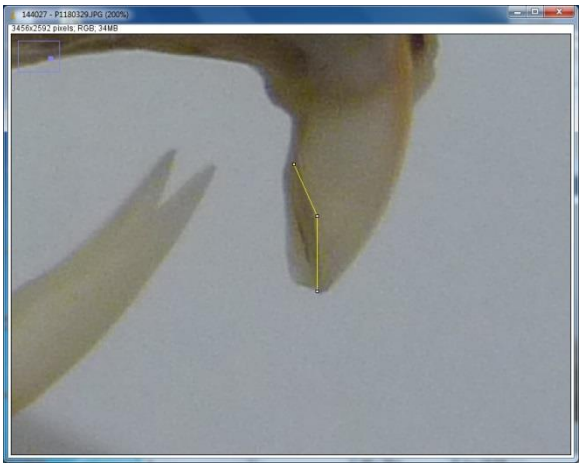
Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

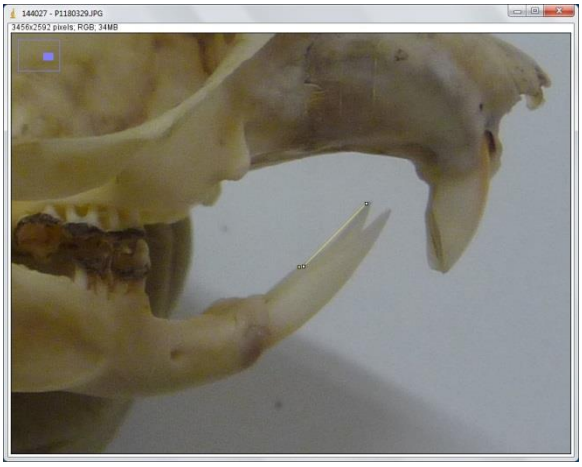
KU 143977 (*Aplodontia rufa*)

Upper Procumbency Angle



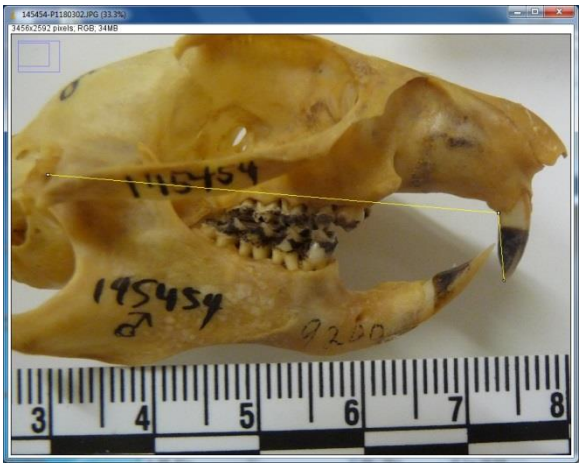
Upper Facet Angle

Lower Procumbency Angle



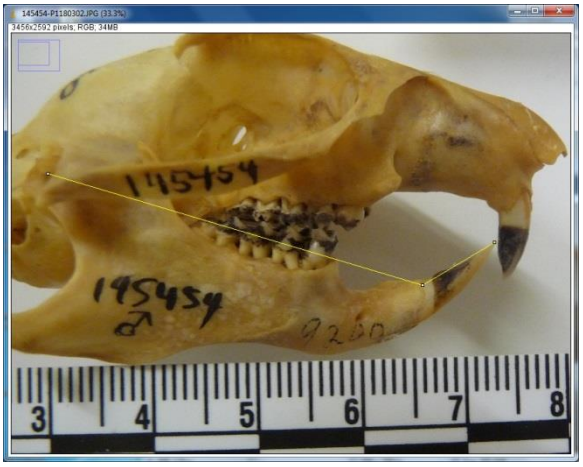
Lower Facet Angle

KU 144027 (*Spermophilus tridecemlineatus*)

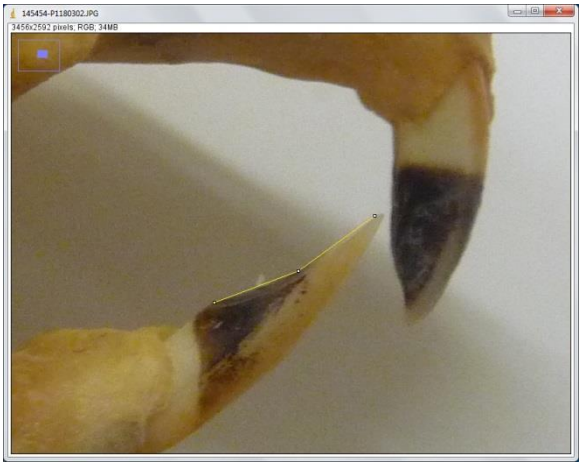


Upper Procumbency Angle

Upper Facet Angle

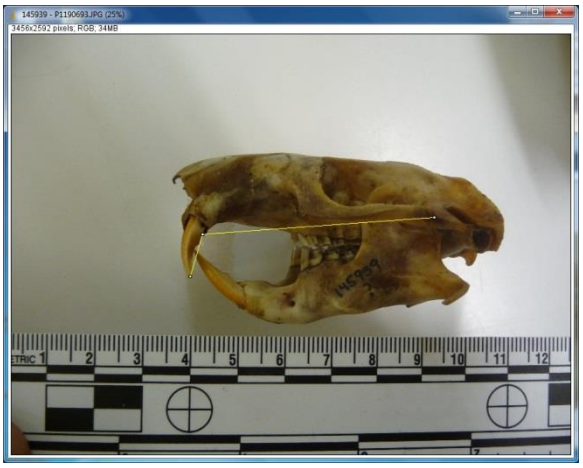


Lower Procumbency Angle

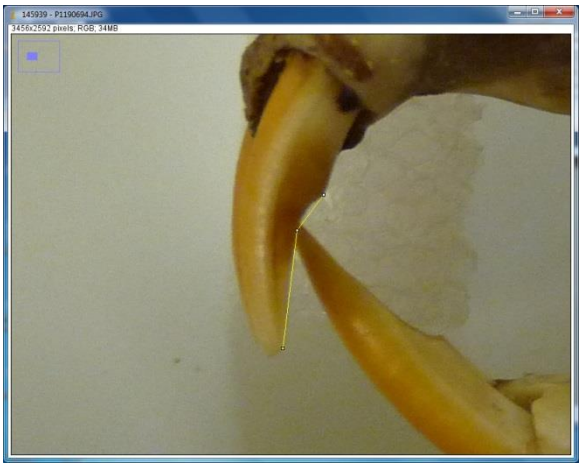


Lower Facet Angle

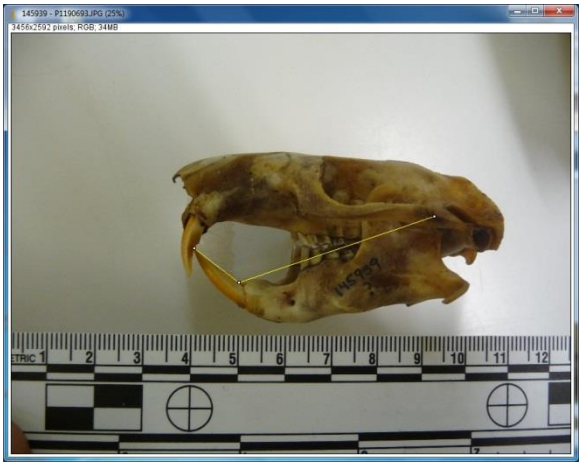
KU 145454 (*Cynomys gunnisoni*)



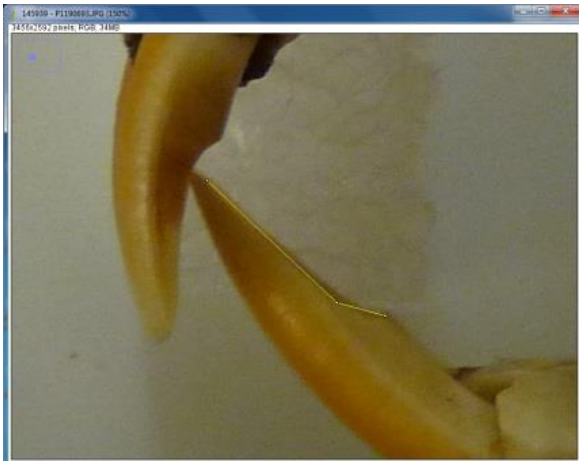
Upper Procumbency Angle



Upper Facet Angle



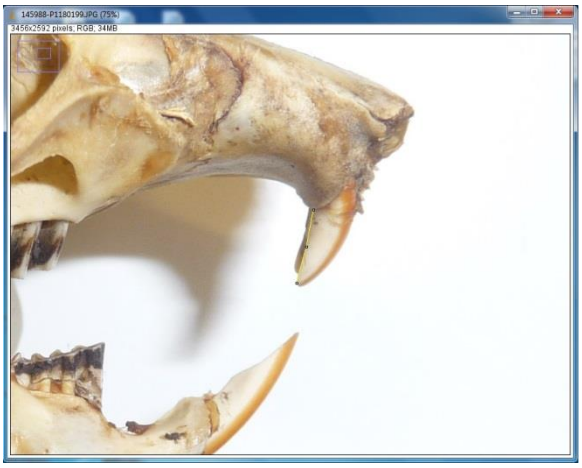
Lower Procumbency Angle



Lower Facet Angle

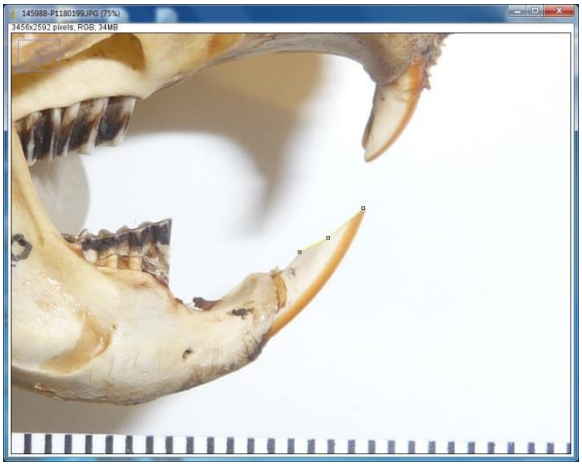
KU 145939 (*Aplodontia rufa*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle



Lower Facet Angle

KU 145988 (*Myospalax myospalax*)

Upper Procumbency Angle

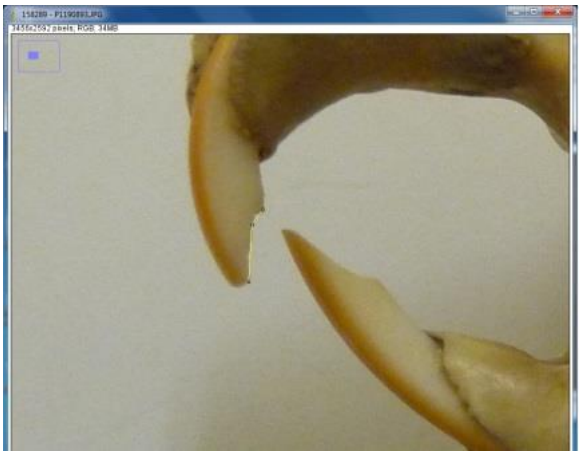
Upper Facet Angle

Lower Procumbency Angle

Lower Facet Angle

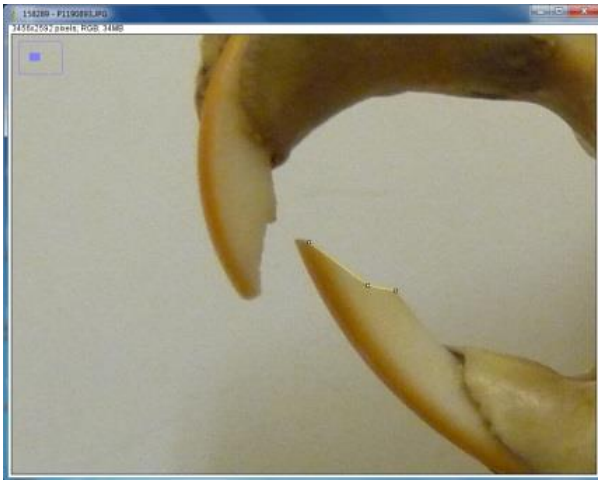
KU 147690 (*Heterocephalus glaber*)

Upper Procumbency Angle



Upper Facet Angle

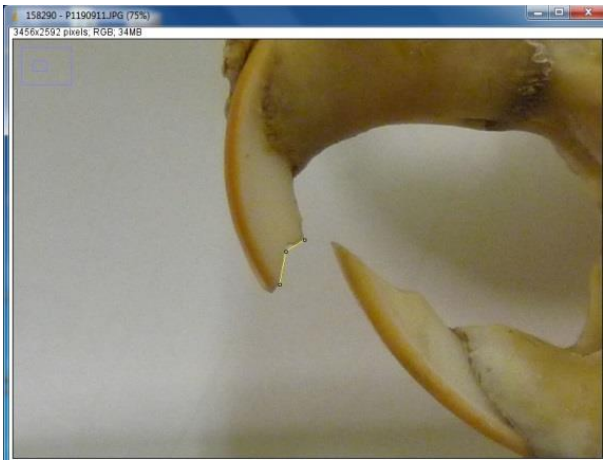
Lower Procumbency Angle



Lower Facet Angle

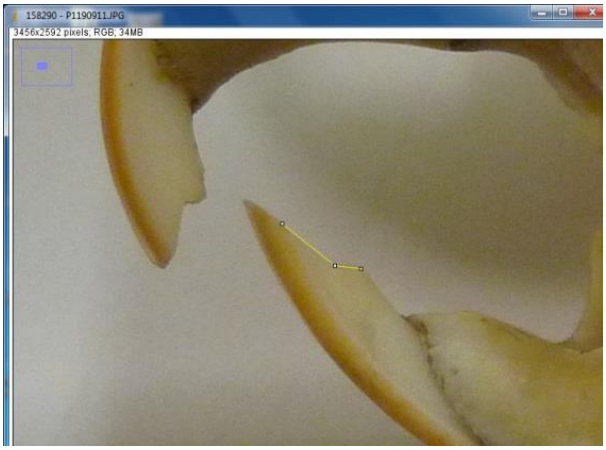
KU 158289 (*Octodon degus*)

Upper Procumbency Angle



Upper Facet Angle

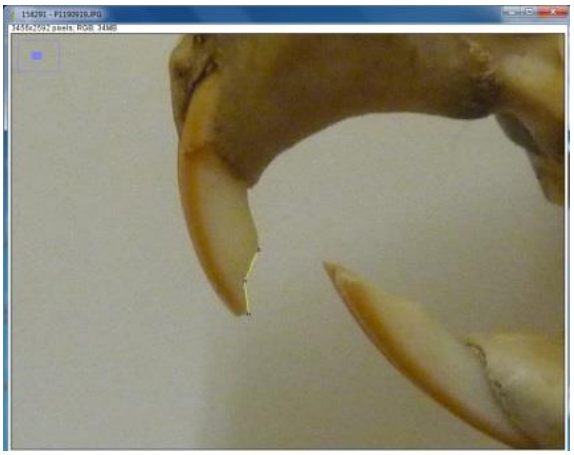
Lower Procumbency Angle



Lower Facet Angle

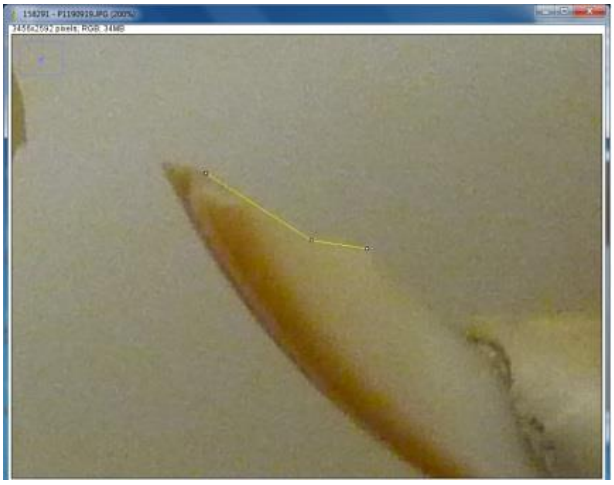
KU 158290 (*Octodon degus*)

Upper Procumbency Angle



Upper Facet Angle

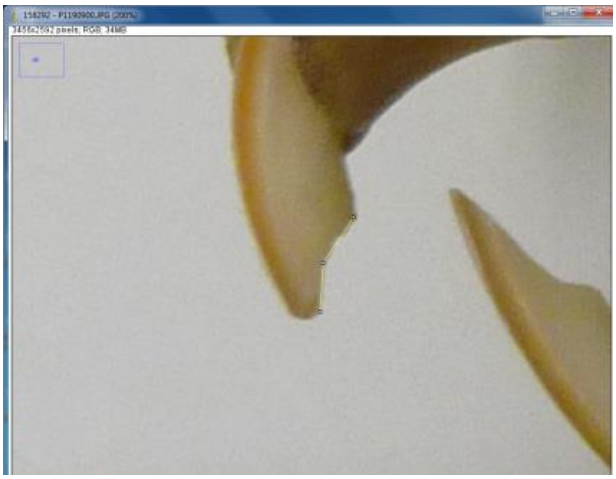
Lower Procumbency Angle



Lower Facet Angle

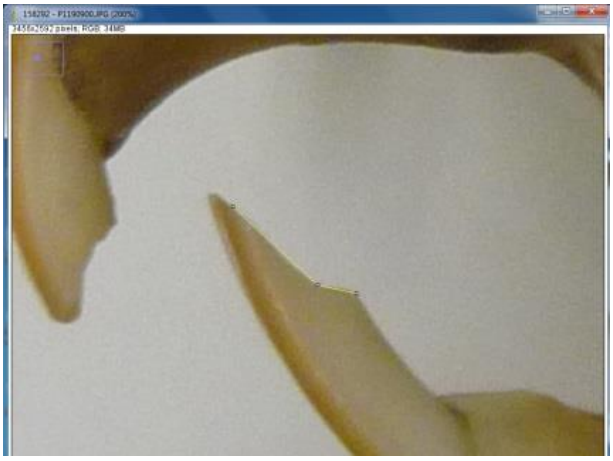
KU 158291 (*Octodon degus*)

Upper Procumbency Angle



Upper Facet Angle

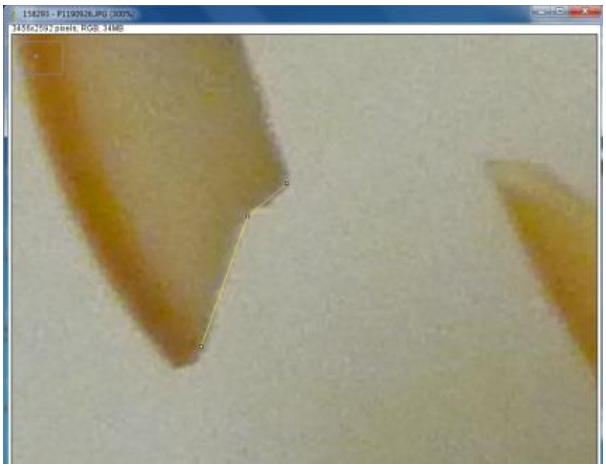
Lower Procumbency Angle



Lower Facet Angle

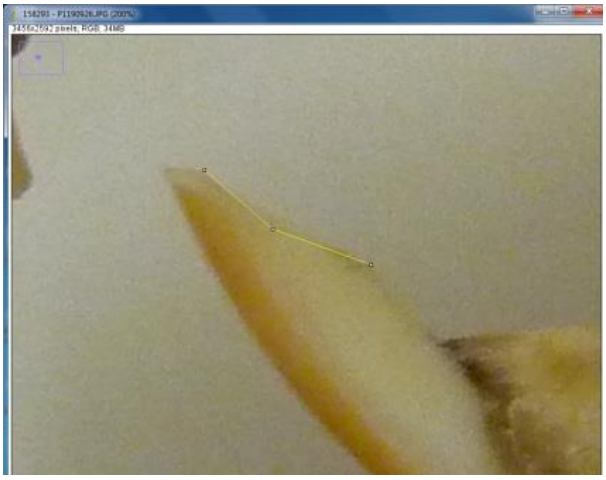
KU 158292 (*Octodon degus*)

Upper Procumbency Angle



Upper Facet Angle

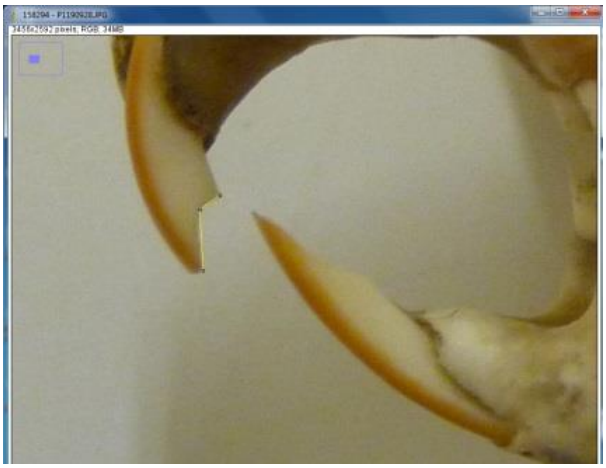
Lower Procumbency Angle



Lower Facet Angle

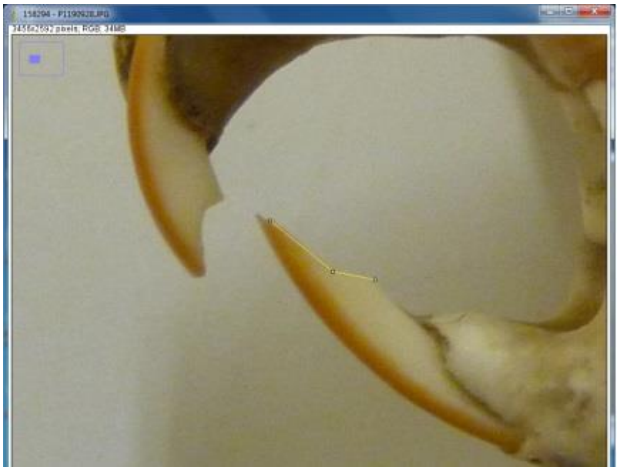
KU 158293 (*Octodon degus*)

Upper Procumbency Angle



Upper Facet Angle

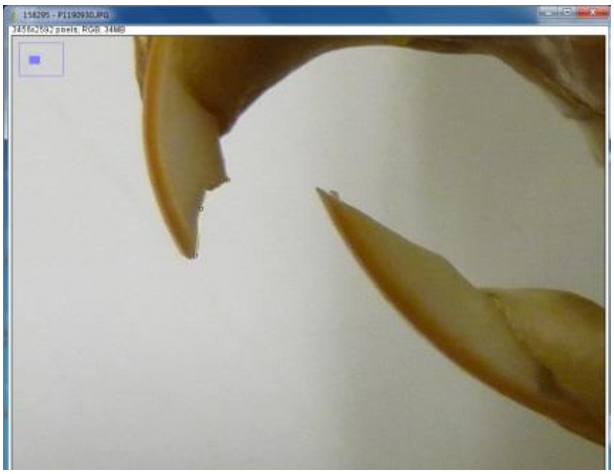
Lower Procumbency Angle



Lower Facet Angle

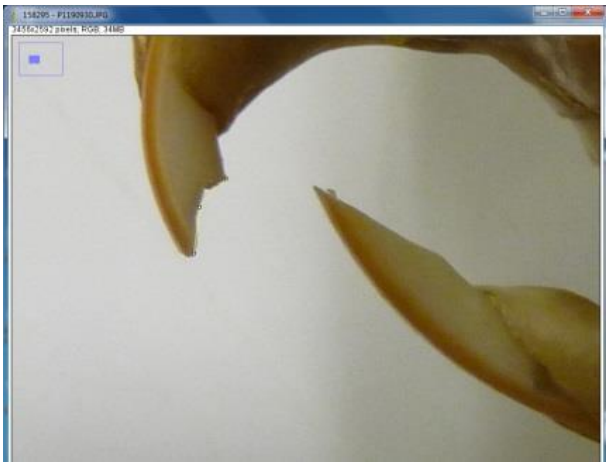
KU 158294 (*Octodon degus*)

Upper Procumbency Angle



Upper Facet Angle

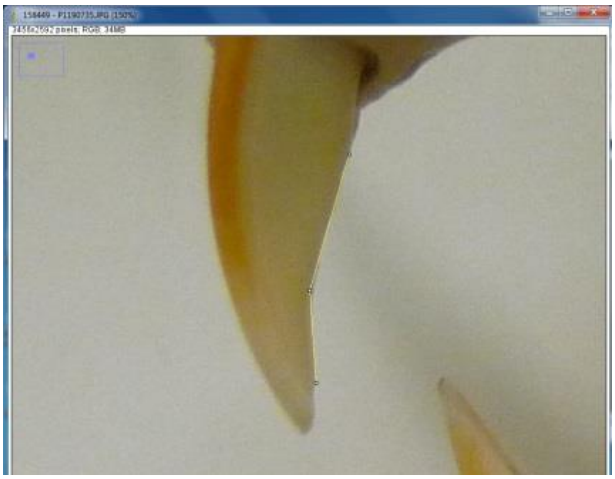
Lower Procumbency Angle



Lower Facet Angle

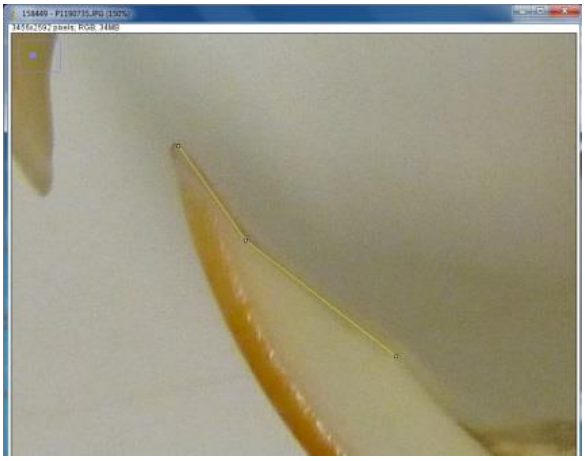
KU 158295 (*Octodon degus*)

Upper Procumbency Angle



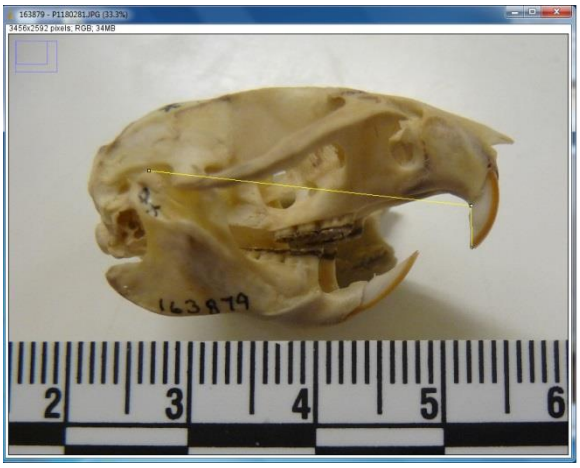
Upper Facet Angle

Lower Procumbency Angle

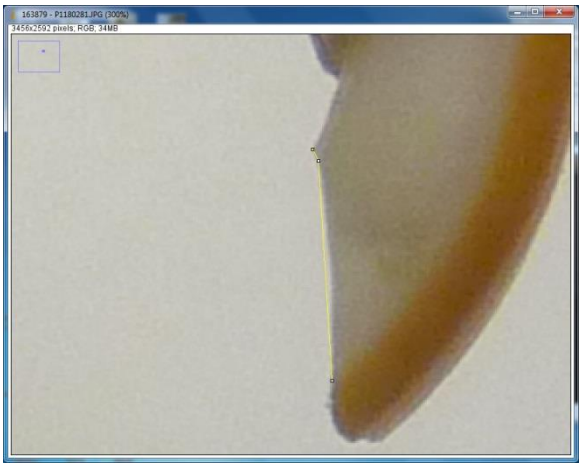


Lower Facet Angle

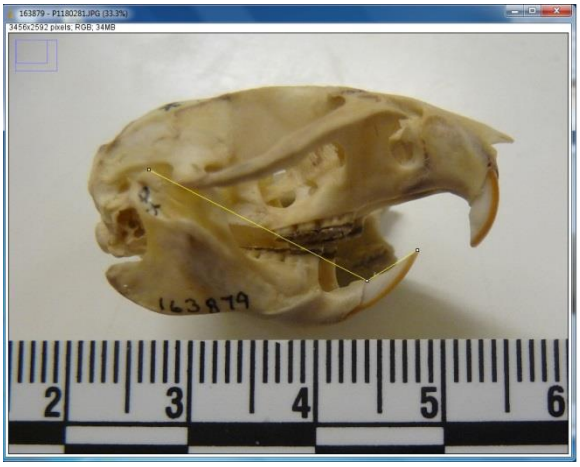
KU 158449 (*Orthogeomys heterodus*)



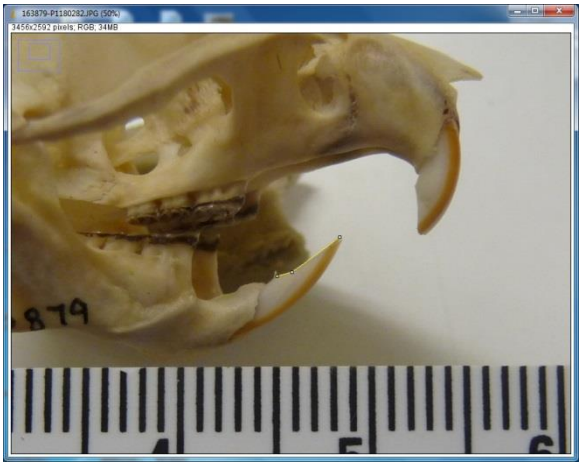
Upper Procumbency Angle



Upper Facet Angle



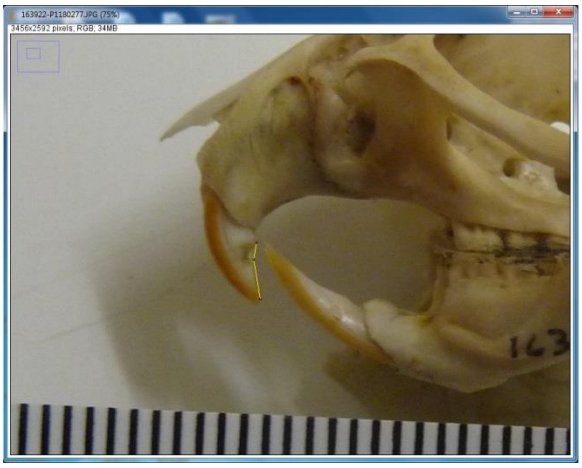
Lower Procumbency Angle



Lower Facet Angle

KU 163879 (*Sigmodon hispidus*)

Upper Procumbency Angle



Upper Facet Angle

Lower Procumbency Angle

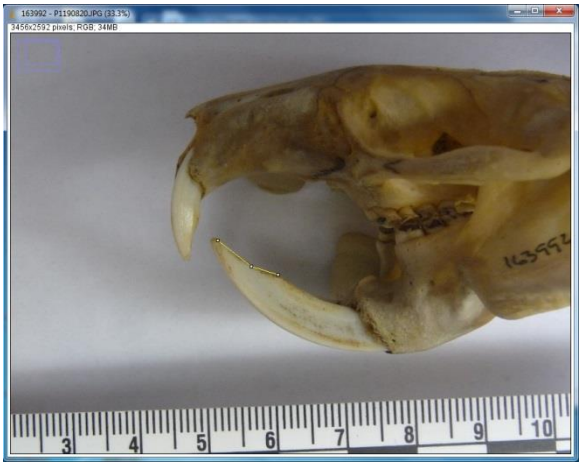
Lower Facet Angle

KU 163922 (*Sigmodon hispidus*)

Upper Procumbency Angle

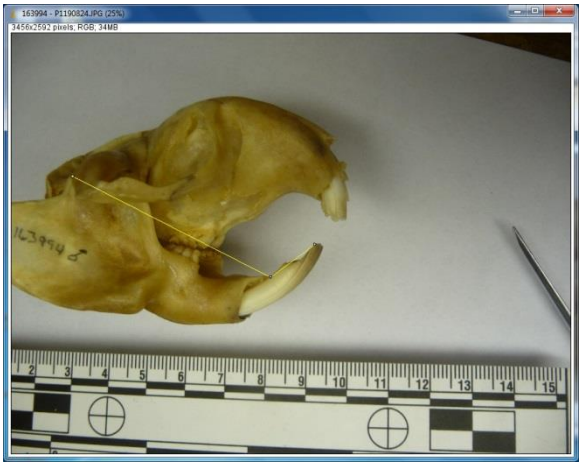
Upper Facet Angle

Lower Procumbency Angle

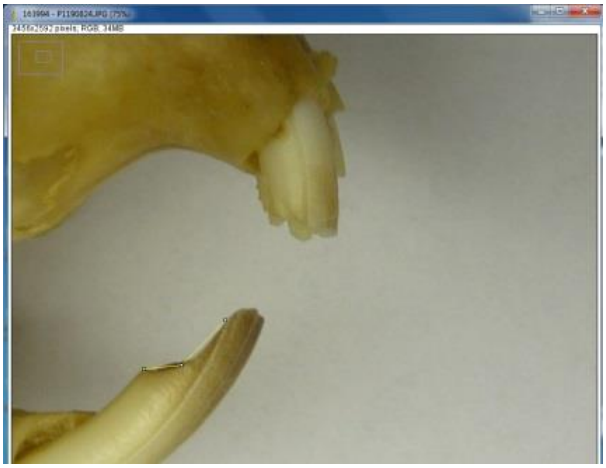


Lower Facet Angle

KU 163992 (*Bathyergus suillus*)

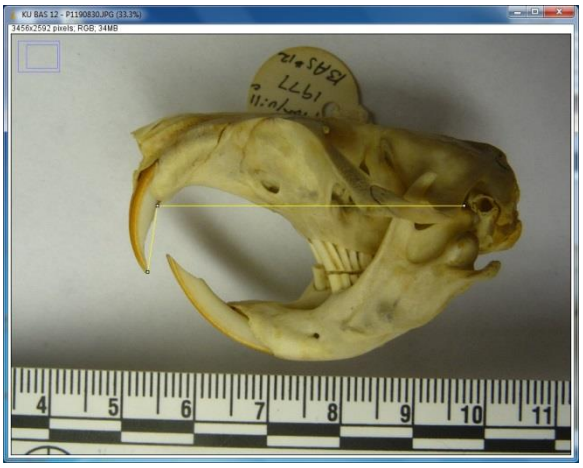


Lower Procumbency Angle

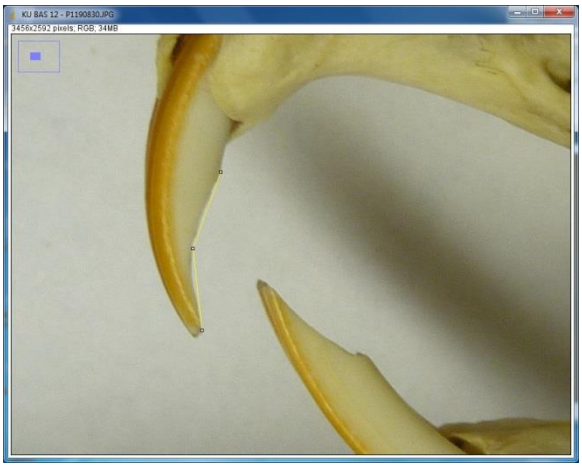


Lower Facet Angle

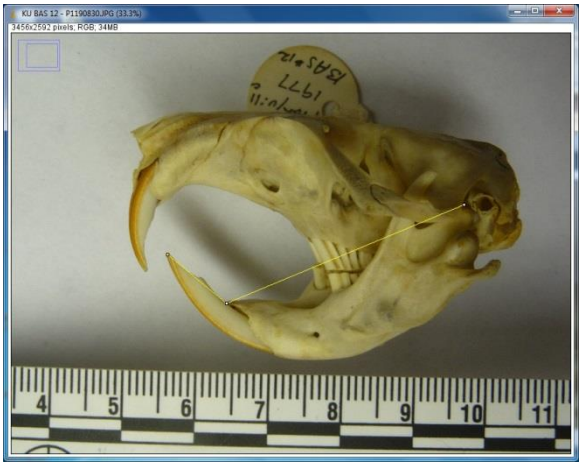
KU 163994 (*Cryptomys mechowi*)



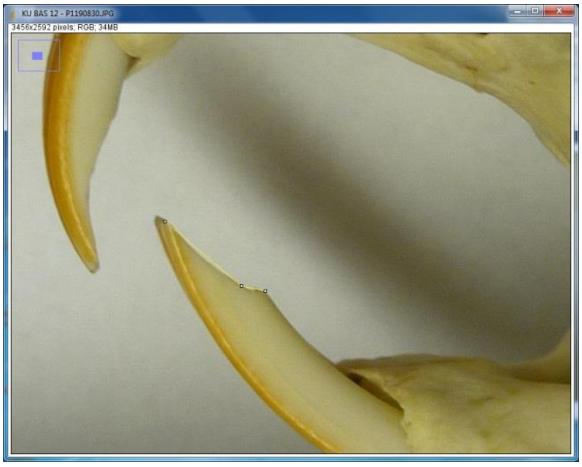
Upper Procumbency Angle



Upper Facet Angle



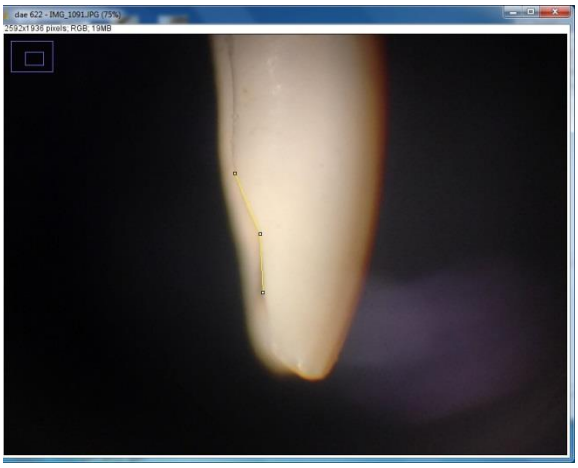
Lower Procumbency Angle



Lower Facet Angle

KU BAS 12 (*Geomys* sp.)

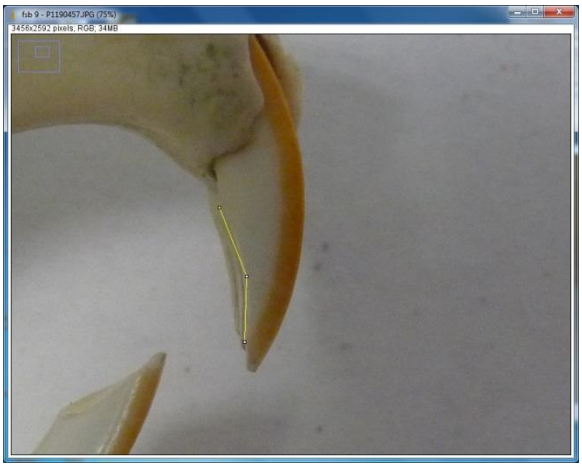
Upper Procumbency Angle



Upper Facet Angle

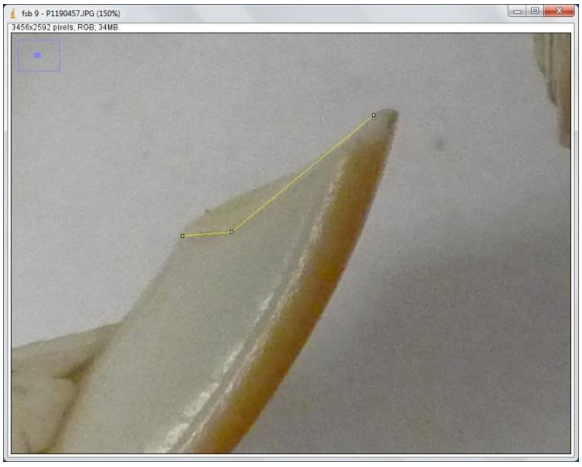
KU DAE 622 (*Thomomys* sp.)

Upper Procumbency Angle



Upper Facet Angle

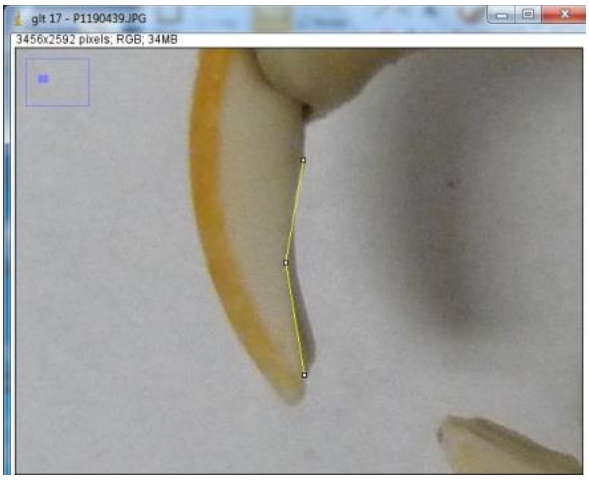
Lower Procumbency Angle



Lower Facet Angle

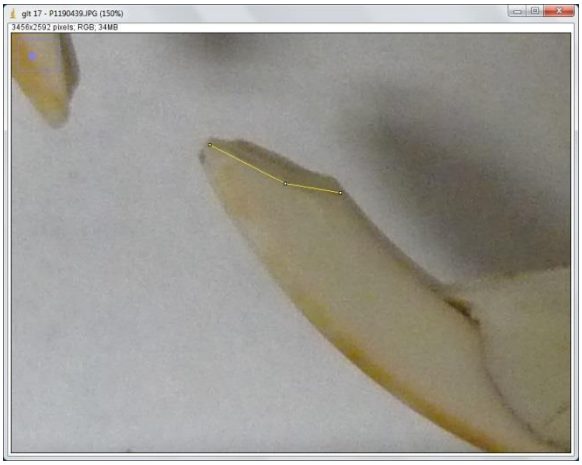
KU FSB 9 (*Geomys bursarius*)

Upper Procumbency Angle



Upper Facet Angle

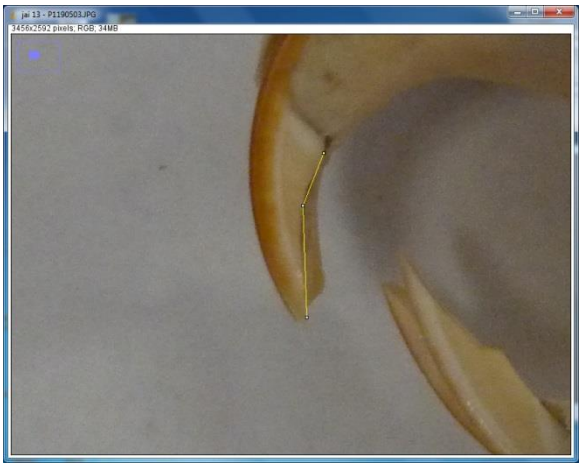
Lower Procumbency Angle



Lower Facet Angle

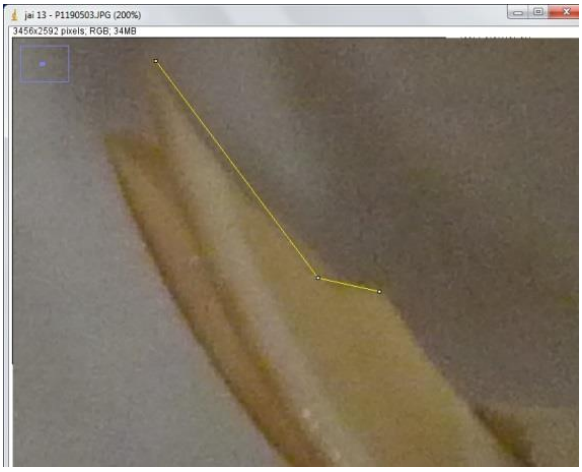
KU GLT 17 (*Geomys bursarius*)

Upper Procumbency Angle



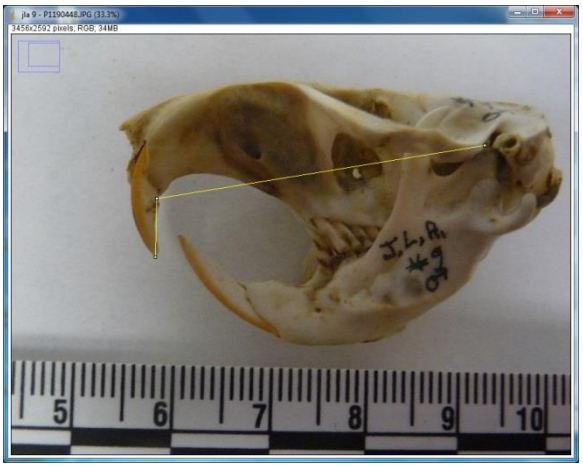
Upper Facet Angle

Lower Procumbency Angle

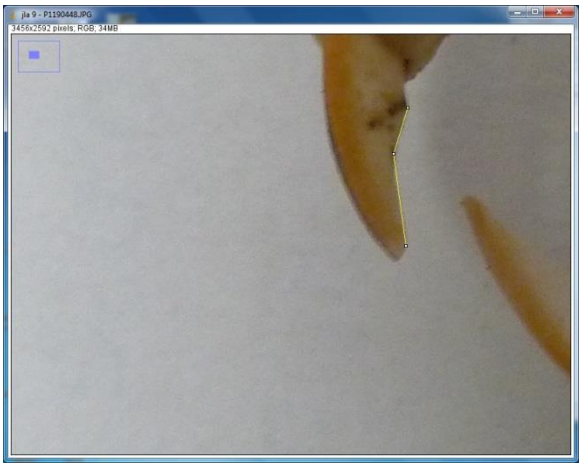


Lower Facet Angle

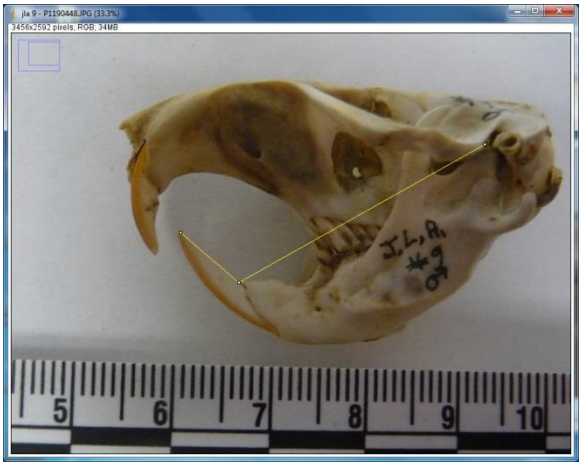
KU JAI 13 (*Geomys bursarius*)



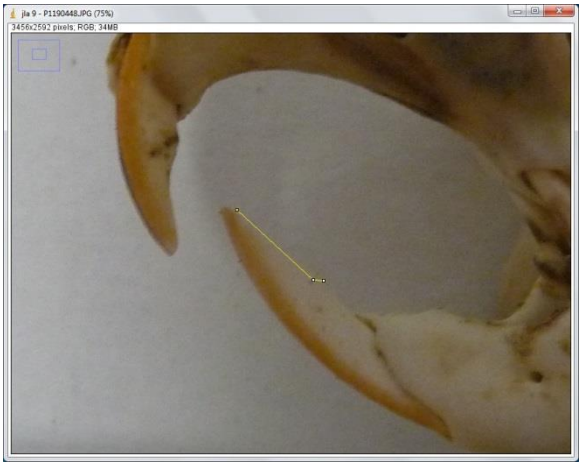
Upper Procumbency Angle



Upper Facet Angle



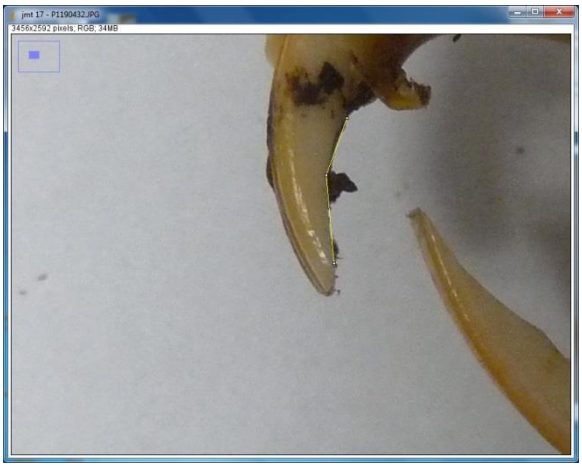
Lower Procumbency Angle



Lower Facet Angle

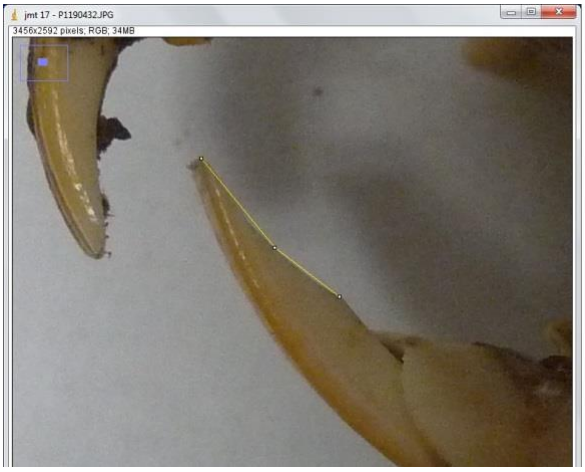
KU JLA 9 (*Geomys bursarius*)

Upper Procumbency Angle



Upper Facet Angle

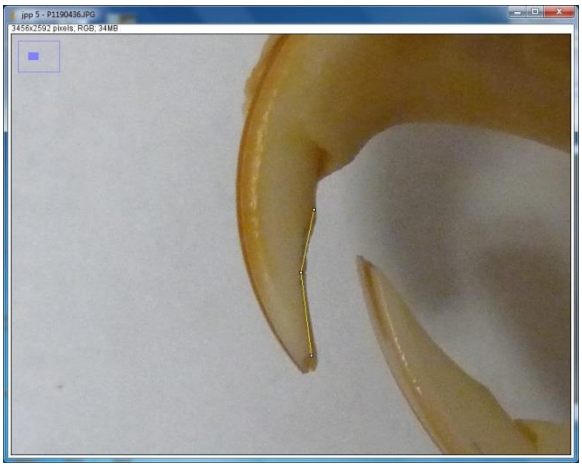
Lower Procumbency Angle



Lower Facet Angle

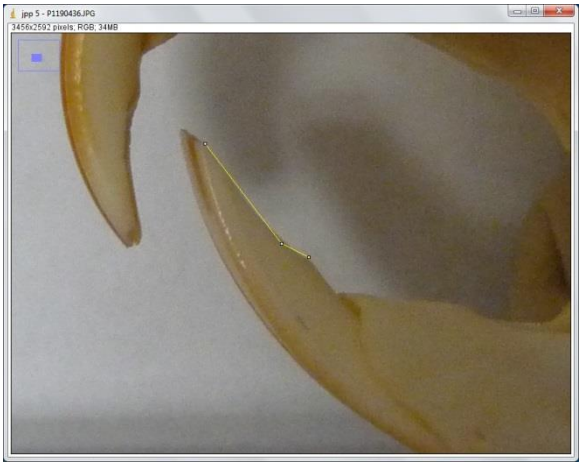
KU JMT 17 (*Geomys bursarius*)

Upper Procumbency Angle



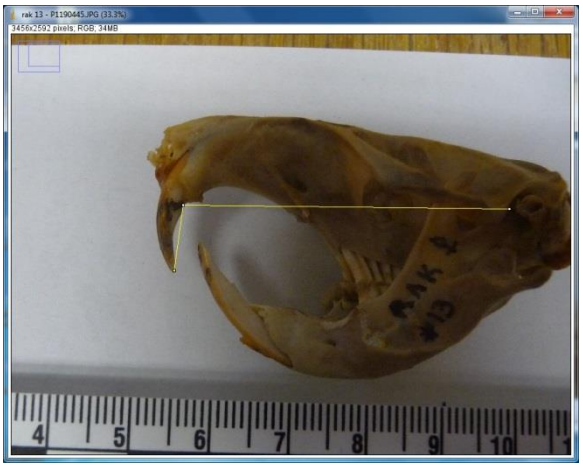
Upper Facet Angle

Lower Procumbency Angle

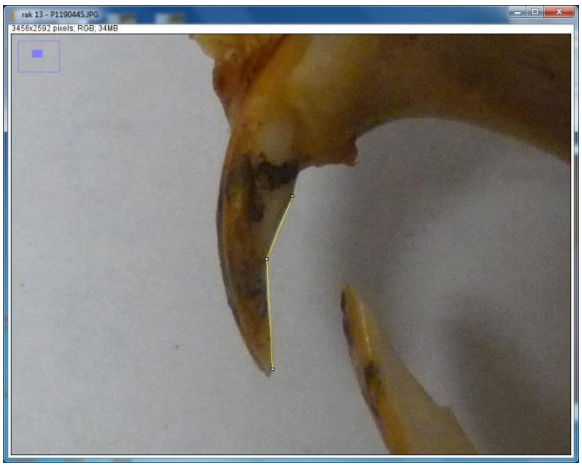


Lower Facet Angle

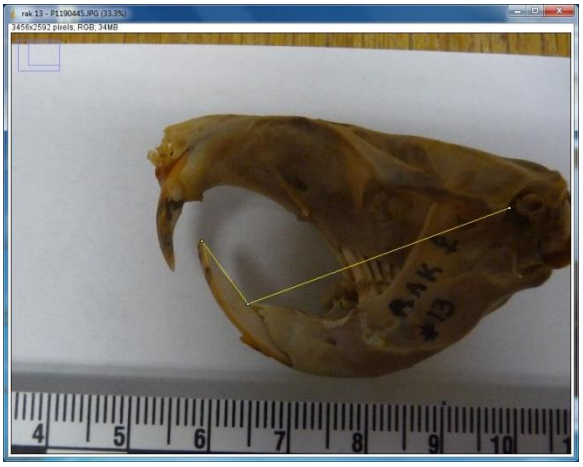
KU JPP 5 (*Geomys bursarius*)



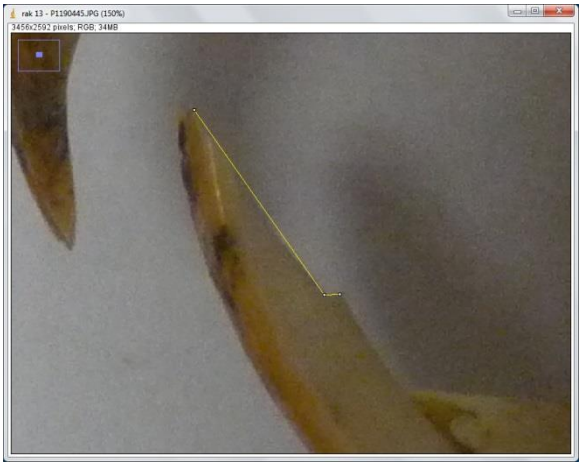
Upper Procumbency Angle



Upper Facet Angle



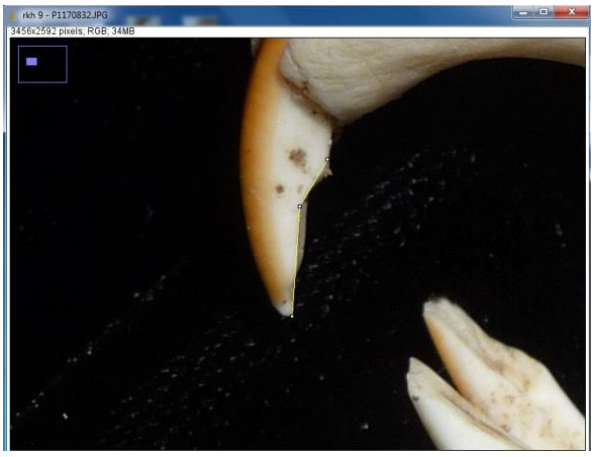
Lower Procumbency Angle



Lower Facet Angle

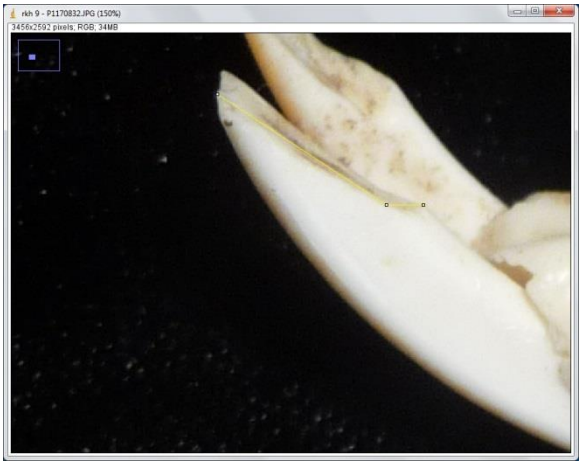
KU RAK 13 (*Geomys bursarius*)

Upper Procumbency Angle



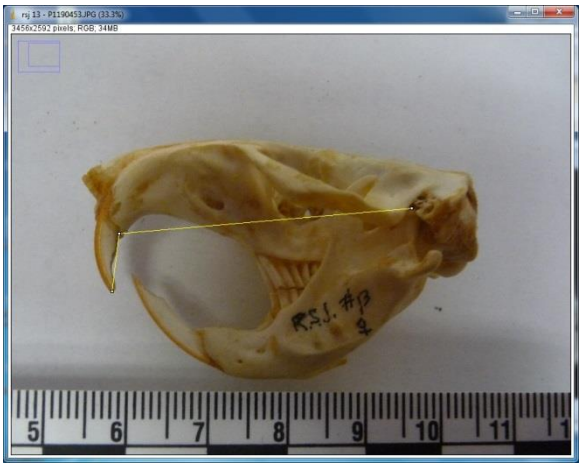
Upper Facet Angle

Lower Procumbency Angle

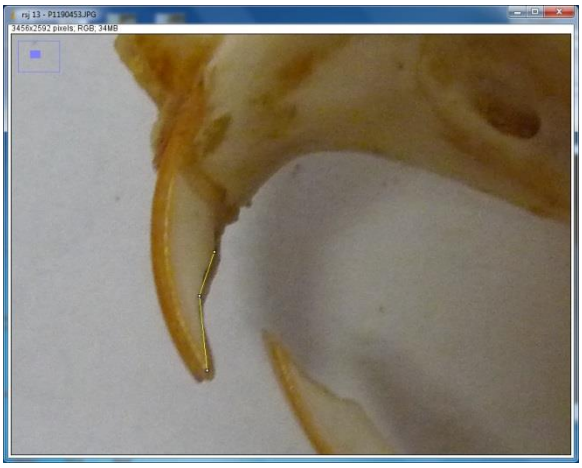


Lower Facet Angle

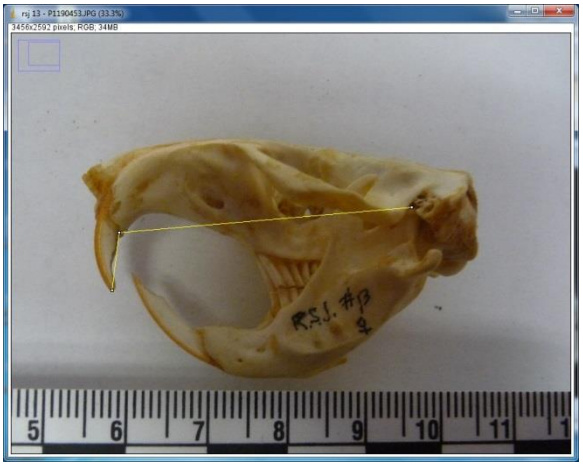
KU RKH 9 (*Geomys bursarius*)



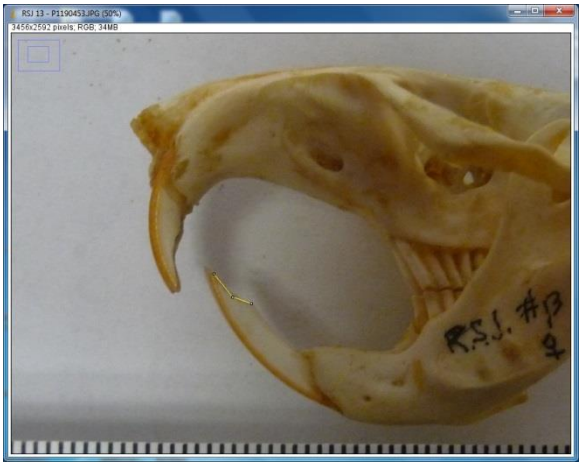
Upper Procumbency Angle



Upper Facet Angle



Lower Procumbency Angle

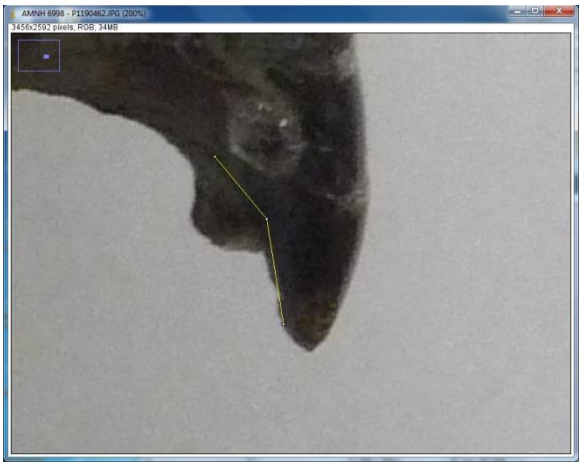


Lower Facet Angle

KU RSJ 13 (*Geomys bursarius*)

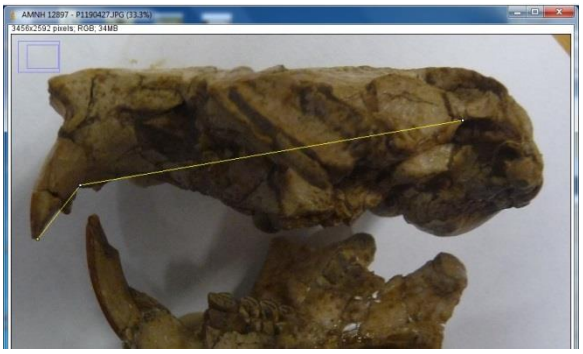
Appendix 12. ImageJ Angle Measurements for Fossil Rodent Skulls

Upper Procumbency Angle

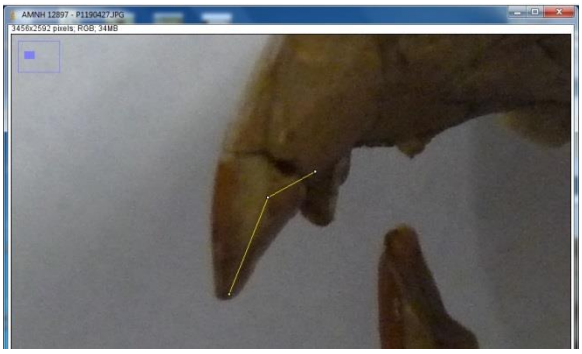


Upper Facet Angle

AMNH 6998 (*Palaeocastor penninsulatus*)



Upper Procumbency Angle



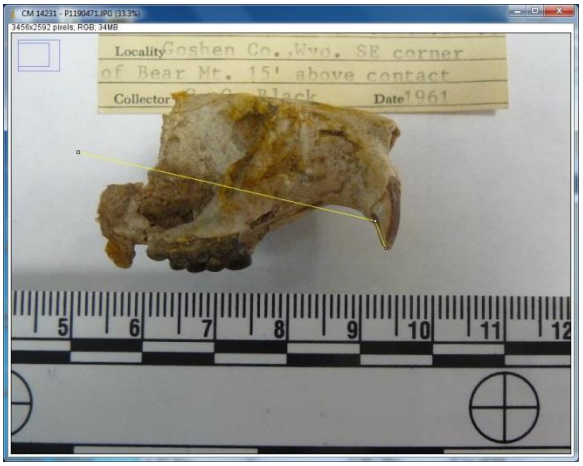
Upper Facet Angle

AMNH 12897 (*Palaeocastor* sp.)

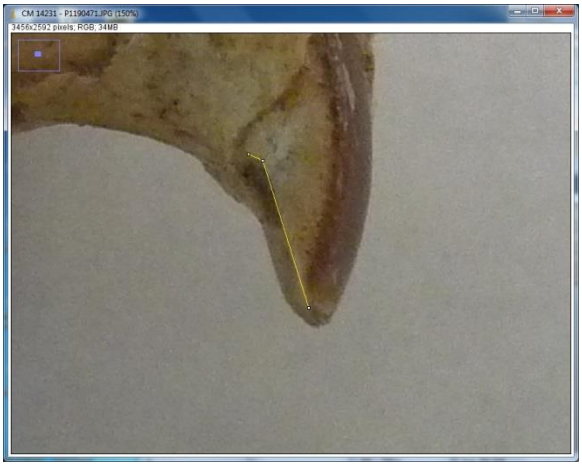
Upper Procumbency Angle

Upper Facet Angle

CM 1220 (*Euhapsis platyceps*)



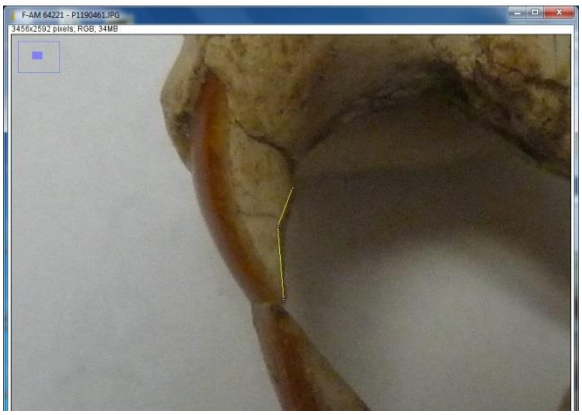
Upper Procumbency Angle



Upper Facet Angle

CM 14231 (*Palaeocastor* sp.)

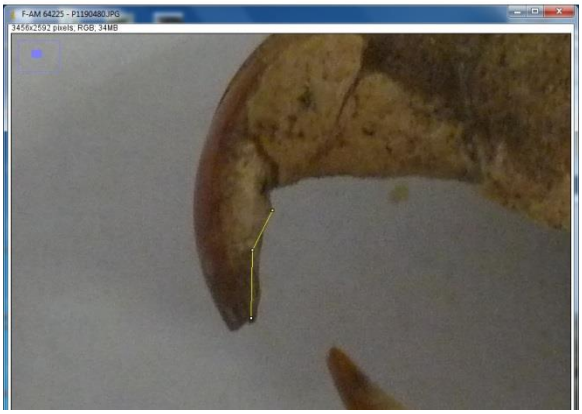
Upper Procumbency Angle



Upper Facet Angle

F:AM 64221 (*Palaeocastor* cf. *nebrascensis*)

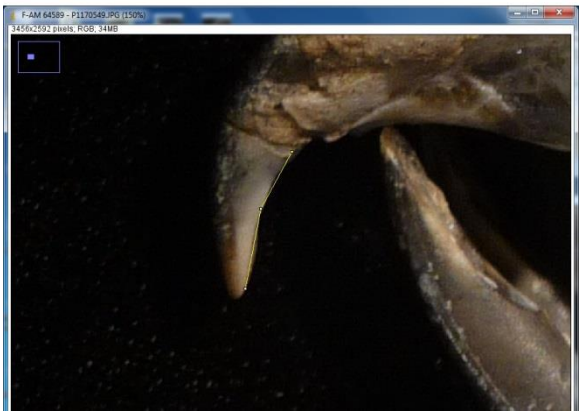
Upper Procumbency Angle



Upper Facet Angle

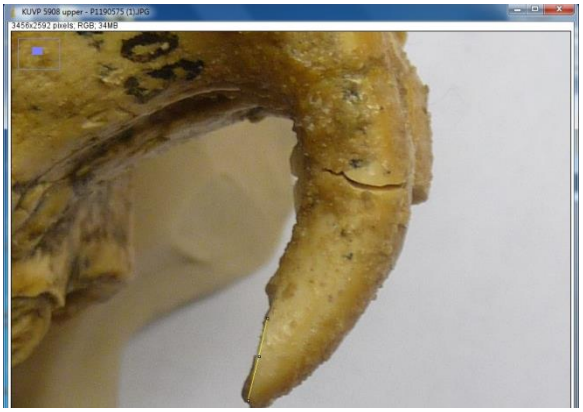
F:AM 64225 (*Palaeocastor* cf. *nebrascensis*)

Upper Procumbency Angle



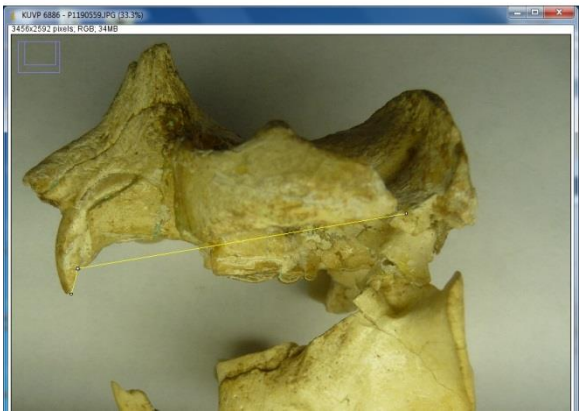
Upper Facet Angle

F:AM 64589 (*Euhapsis luskensis*)

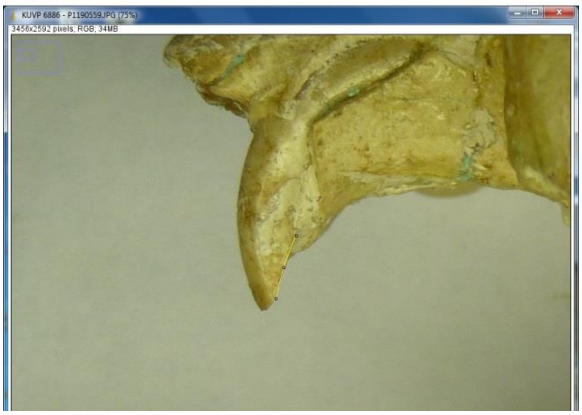


Upper Facet Angle

KUVP 5908 (*Ceratogaulus* sp.)



Upper Procumbency Angle



Upper Facet Angle

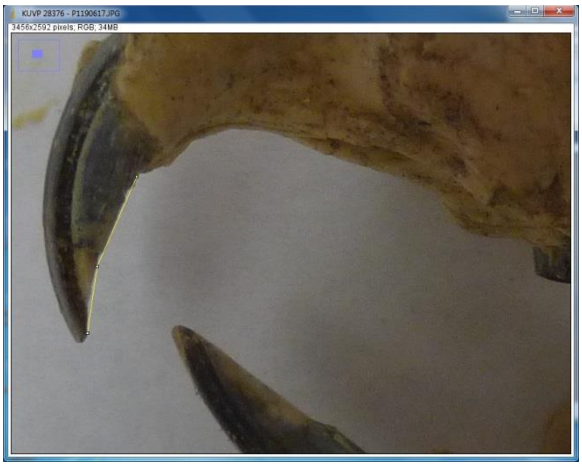
KUVP 6886 (*Ceratogaulus minor*)

Upper Procumbency Angle

Upper Facet Angle

KUVP 28372 (*Palaeocastor fossor*)

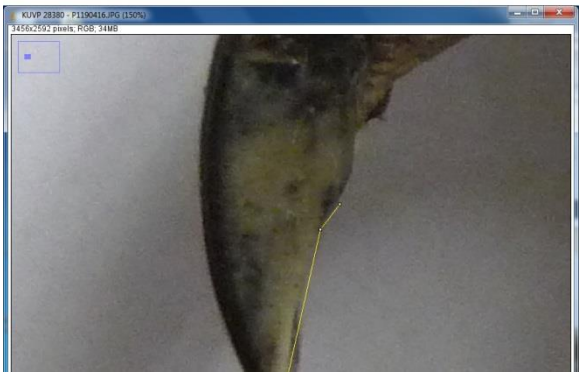
Upper Procumbency Angle



Upper Facet Angle

KUVP 28376 (*Paraeuhapsis breugerorum*)

Upper Procumbency Angle



Upper Facet Angle

KUVP 28380 (*Palaeocastor* (*Capacikala*) *magnus*)

Upper Procumbency Angle

Upper Facet Angle

KUVP 28383 (*Palaeocastor fossor*)

Upper Procumbency Angle

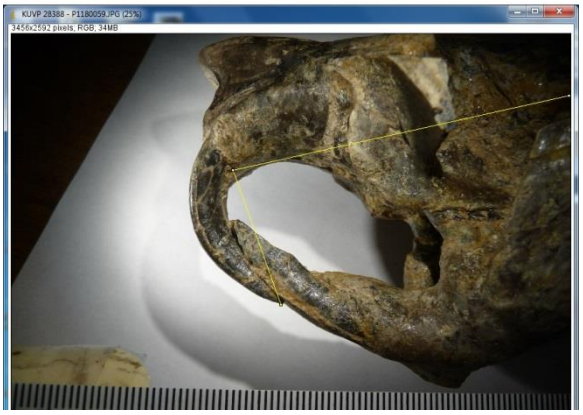
Upper Facet Angle

KUVP 28385 (*Palaeocastor fossor*)

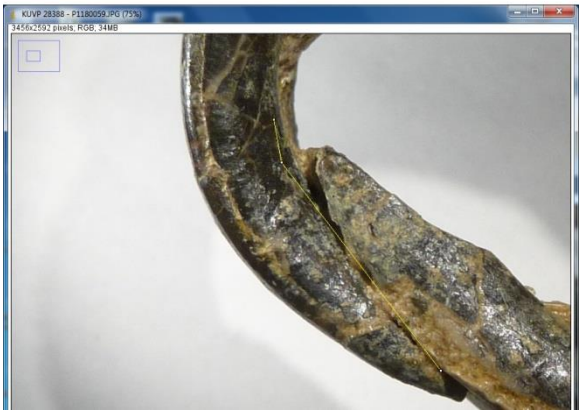
Upper Procumbency Angle

Upper Facet Angle

KUVP 28386 (*Palaeocastor* (*Capacikala*) *magnus*)



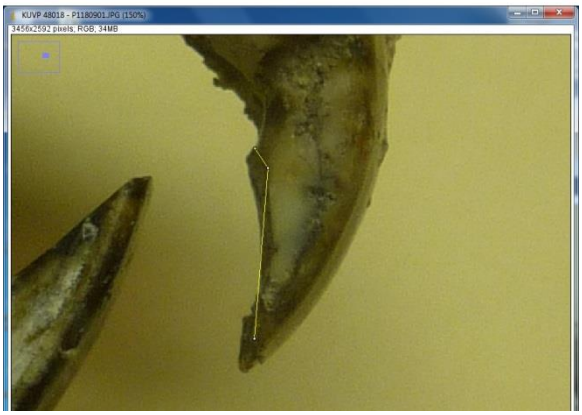
Upper Procumbency Angle



Upper Facet Angle

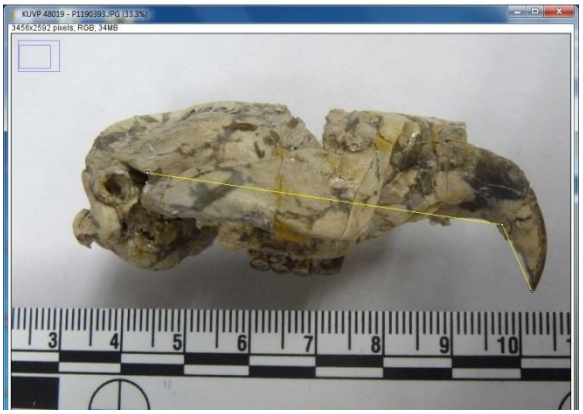
KUVP 28388 (*Palaeocastor* (*Capacikala*) *magnus*)

Upper Procumbency Angle



Upper Facet Angle

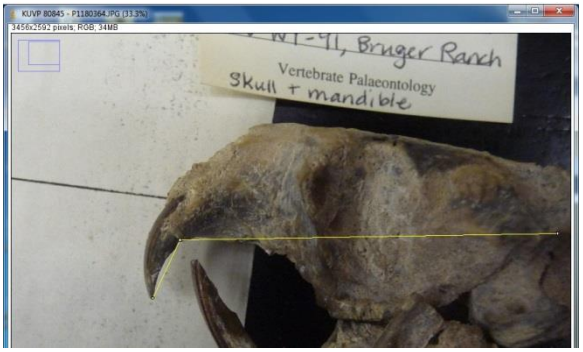
KUVP 48018 (*Pseudopalaeocastor barbouri*)



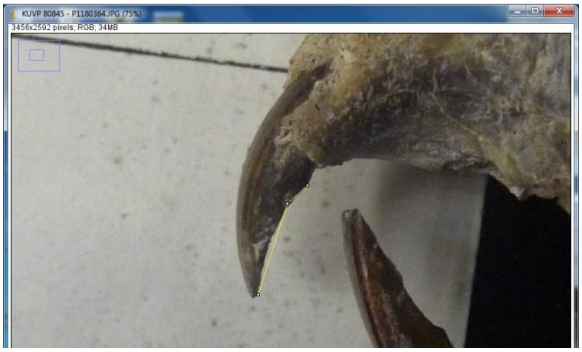
Upper Procumbency Angle

Upper Facet Angle

KUVP 48019 (*Palaeocastor fossor*)



Upper Procumbency Angle



Upper Facet Angle

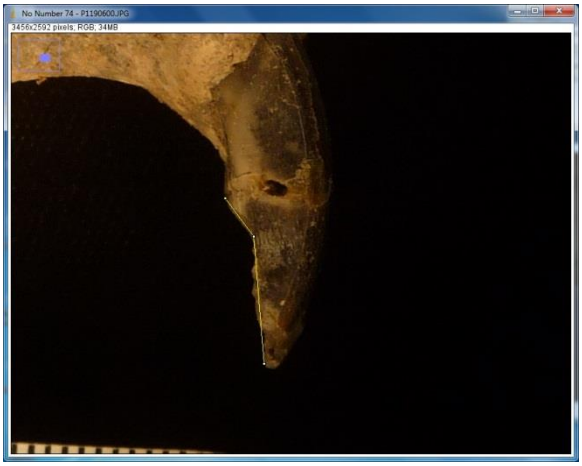
KUVP 80845 (*Fossorcastor greeni*)

Upper Procumbency Angle

Upper Facet Angle

KUVP 125061 (unnamed new taxon)

Upper Procumbency Angle



Upper Facet Angle

KUVP 155839 (*Palaeocastor* sp.)